HOW ACUTE STRESS DURING CONSOLIDATION AFFECTS MEMORY FOR NEGATIVE MATERIALS WITH DIFFERENT AROUSAL LEVELS

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HOW ACUTE STRESS DURING CONSOLIDATION AFFECTS MEMORY FOR NEGATIVE MATERIALS WITH DIFFERENT AROUSAL LEVELS

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SUMMARY

Both human and animal research has demonstrated that acute stress affects memory, and the nature of this effect depends on when the stress occurs. Stress during consolidation consistently enhances memory, but there is disagreement as to whether memory for emotional or neutral information is improved. The animal research suggests that only memory for emotionally arousing information is enhanced following stress during consolidation. However, human studies have found memory improvements for both emotional and neutral information. According to theory based on animal research, memory for the most arousing material should be enhanced as a result of stress during consolidation. Because of this discrepancy between the animal and the human literature, the current study investigated the effect of acute psychological stress on memory for both low arousal and high arousal negative stimuli. We predicted that stress during consolidation would enhance memory, particularly for the high arousal negative stimuli. We found that stress did not have an effect on item memory performance and that stress actually reduced participant's confidence in their memory.

CHAPTER 1

INTRODUCTION

1.1 Physiology of Stress

Stress is something we all experience at some point in our lives and can be broadly defined as our body and brain's response to changing demands (de Kloet, Joels, & Holsboer, 2005). When we feel stress, we experience a set of physiological changes that are collectively known as the stress response. This stress response is mediated by two networks: the Sympathetic-Adrenal-Medulla (SAM) axis and the Hypothalamic-Pituitary-Adrenal (HPA) axis. The sympathetic nervous system (SNS) controls the SAM axis, which is the initial rapid response to stress. Activation of the SAM axis leads to the release of epinephrine and norepinephrine from the adrenal medulla. The HPA axis is a second slower response that leads to the secretion of glucocorticoids (cortisol in humans) from the adrenal cortex (for review, see Wolf, 2008).

There are different types of stress. Stress can either be chronic or acute. Chronic stress lasts for a long period of time and is generally harmful to both health and cognitive processes. On the other hand, acute stress is short in duration and can be beneficial to cognitive processes, such as memory. Stress can also be physical or psychological. Physical stress (e.g., pain) primarily impacts the body, whereas psychological stress (e.g., fear) mostly affects the mind. Laboratory studies of acute stress have used both physical and psychological stressors to induce stress. While stressors can take many forms, there are certain characteristics that make a stressor more likely to elicit a substantial and reliable cortisol response. The two important factors for this are uncontrollability and social evaluative threat (Dickerson & Kemeny, 2004). Uncontrollability means that the

participants are unable to change anything that might alleviate the stress. This can include tasks that are impossible to perform successfully or the unremitting presence of a loud noise or other sensory distracters. Social evaluative threat refers to the presence of a negative social comparison. This often involves the presence of people other than the experimenter who are judging the participant's performance. Stress tasks that incorporate both of these factors are desirable in experimental settings, because these tasks should reliably produce a robust increase in cortisol (Dickerson & Kemeny, 2004).

1.2 Stress Effects for Different Phases of Memory

Studies examining the effects of acute stress on memory have found that acute stress can be helpful in some situations and harmful in others. One of the key factors determining whether stress will result in improvements or impairments is when the stress occurs (for review, see Wolf, 2009). Long-term memory can be separated into three phases: encoding, when information is learned, consolidation, when information is stored and the memory trace is strengthened, and retrieval, when the information is remembered.

There is consistent evidence from studies administering a stressor immediately after encoding that acute stress during consolidation can improve memory performance (for review, see Wolf, 2008). The first study in humans to suggest that stress during consolidation can be beneficial to memory was a study that administered epinephrine intravenously immediately following learning (Cahill & Alkire, 2003). Participants who received 80 ng/kg/min of epinephrine had higher recall for negative pictures one week later than participants who received saline. Since this first study, others have found additional support for the enhancing effect of acute stress during consolidation on long-

term memory (Beckner, Tucker, Delville, & Mohr, 2006; Cahill, Gorski, & Le, 2003; Preuss & Wolf, 2009; Smeets, Otgaar, Candel, & Wolf, 2008). For example, Smeets and colleagues (2008) manipulated when stress occurred to looked for different effects on episodic memory. They included three stress groups, with a cold pressor stress (holding a hand in cold water for several minutes) administered either immediately before encoding, during consolidation, or immediately before retrieval. After a 24 hour delay, the participants who received the stress during consolidation recalled more negative words than the participants who were not stressed as well as participants in the encoding stress and retrieval stress groups on a cued recall test.

The human research showing that stress during consolidation can improve memory is consistent with animal research, which demonstrates a beneficial effect on memory with the administration of acute stress and elevated glucocorticoid levels during consolidation (Roozendaal, 2002). Increases in levels of glucocorticoids (cortisol in humans) following stress appear to be critical for the memory enhancing effects, as glucocorticoid release facilitates noradrenergic activity in the basolateral nucleus of the amygdala (BLA), an area that is important for memory consolidation (McGaugh & Roozendaal, 2002). The timing of the stressor in the early consolidation period appears to be critical for these effects, as injections of glucocorticoids only enhance long-term memory when administered shortly after training, but not several hours following training (Flood et al., 1978; Kovacs, Telegdy, & Lissak, 1977; Roozendaal & McGaugh, 1996; Roozendaal, Williams, & McGaugh, 1999). The reason for this is that memories are fragile in the early consolidation period and thus vulnerable to influence from many different factors, including stress hormones (Roozendaal, 2002).

There is also an adaptive reason why stress during consolidation would enhance memory for events that occurred immediately prior to the stress. Stressors that animals encounter in the wild are often threats to the animal's survival, such as being chased by a predator. Remembering what occurred before that threatening event could be useful in predicting and preventing threats in the future. An animal could use their enhanced memory of what preceded a threat to recognize similar events in the future and do something to avoid the threat, such as hiding from a predator. The animals that are more successful at this process would be more likely to survive and reproduce.

The effect of acute stress before or during encoding is unclear, with some studies finding memory enhancing effects (Abercrombie, Kalin, Thurow, Rosenkranz, & Davidson, 2003; Buchanan & Lovallo, 2001; Schwabe, Bohringer, Chatterjee, & Schachinger, 2008), some finding memory impairing effects (Maheu, Collicutt, Kornik, Moszkowski, & Lupien, 2005; Maheu, Joober, Beaulieu, & Lupien, 2004; Payne et al., 2006; Schwabe & Wolf, 2010), and others finding a combination of memory enhancing and memory impairing effects (Kuhlmann & Wolf, 2006; Payne et al., 2007). The studies that find memory enhancing effects with stress during encoding can be viewed as consistent with the beneficial effects of acute stress at consolidation. When someone is stressed either before or during encoding, their cortisol levels remain elevated into the early consolidation period. Because the increase in cortisol appears to be critical for memory enhancing effects in rodents (for review, see Roozendaal, McEwen, & Chattarji, 2009), having elevated cortisol levels during consolidation may be more important than administering stress during consolidation for producing memory enhancing effects.

The most cited explanation for why some studies have found impairing effects for stress during encoding is that stress before or during encoding may create a divided attention situation, in which participants must simultaneously try to learn the material and cope with the stress. Divided attention during encoding consistently lowers memory performance (Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Fernandes & Moscovitch, 2000; Foerde, Knowlton, & Poldrack, 2006; Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000; Naveh-Benjamin, Guez, & Marom, 2003), so if this occurs with stress it would result in worse memory. It is not clear why stress before encoding would sometimes create a divided attention situation some but not all of the time. What is clear is that the memory benefits from acute stress consistently occur following stress during consolidation and not stress before encoding.

Acute stress that occurs immediately prior to memory retrieval consistently impairs memory performance (Buchanan, Tranel, & Adolphs, 2006; de Quervain, Aerni, & Roozendaal, 2007; de Quervain et al., 2003; de Quervain, Roozendaal, Nitsch, McGaugh, & Hock, 2000; Kuhlmann, Kirschbaum, & Wolf, 2005; Schwabe et al., 2009; Smeets et al., 2008). These effects appear to be driven by cortisol, the same hormone implicated in the beneficial effects of stress during consolidation, as increases in cortisol during retrieval have been correlated with memory impairment (Buchanan et al., 2006). Evidence from animal studies suggests that elevated glucocorticoid levels may block retrieval processes in the hippocampus, which has a high density of glucocorticoid receptors, by reducing the firing rate of hippocampal neurons (Roozendaal, 2002).

Overall, when acute stress occurs changes what kind of effect stress will have on episodic memory. Stress before encoding has a mixed effect, with some evidence for

memory impairments (Maheu et al., 2005; Maheu et al., 2004; Payne et al., 2006; Schwabe & Wolf, 2010) and some evidence for memory improvements (Abercrombie et al., 2003; Buchanan & Lovallo, 2001; Schwabe, Bohringer, et al., 2008). Stress before retrieval consistently impairs memory (Buchanan et al., 2006; de Quervain et al., 2007; de Quervain et al., 2003; de Quervain et al., 2000; Kuhlmann, Piel, & Wolf, 2005; Smeets et al., 2008), while stress during consolidation consistently enhances memory (Beckner et al., 2006; Cahill et al., 2003; Preuss & Wolf, 2009; Smeets et al., 2008). We focused on effects of stress during consolidation on memory, because we were more interested in investigating memory improvements than memory impairments. Looking for way to improve memory is useful for developing interventions for groups that experience memory problems, such as older adults.

1.3 Emotional Content and Stress Effects

Emotion is an important factor in determining what we remember. Memory for emotional material is generally superior to memory for neutral material (for review, see Talmi, 2013). While this effect is found for both positive and negative materials, negative information is more likely to be remembered with greater detail than either neutral or positive information (Kensinger & Schacter, 2008). Interestingly, there is also a relationship between the effect of stress on memory and emotion. The connection between emotion and stress is likely because of the role of the amygdala in both emotional memory and the effects of stress on memory (McGaugh, 2004).

Animal research on how stress affects memory suggests that emotional arousal is necessary for the enhancing effects observed with stress during consolidation (Roozendaal, 2002). Stress during consolidation will selectively enhance emotionally

arousing memories, such as the place the rodent received a foot-shock or the location of an escape platform in a water maze (Roozendaal et al., 2009). Epinephrine, which is released peripherally following both stress and emotional arousal, leads to an increase in noradrenergic activity in the basolateral nucleus of the amygdala (BLA) by activating vagal afferents of the nucleus of the solitary tract (McGaugh & Roozendaal, 2002). This noradrenergic activity appears to be crucial for the memory enhancing effects of stress during consolidation, as direct infusions of noradrenaline into the BLA immediately following learning enhances consolidation and later memory of emotionally arousing events (Roozendaal et al., 2009).

Emotional valence affects the interaction between stress and memory. Some studies have found that acute stress during consolidation selectively enhanced memory for emotional materials (Cahill & Alkire, 2003; Cahill et al., 2003; Smeets et al., 2008). For example, Smeets and colleagues (2008) found that memory for negative emotional words was enhanced for the stress during consolidation group compared to the no stress group, but memory for neutral words was the same across groups. Cahill and colleagues (2003) stressed participants with a cold pressor during consolidation and found that the participants who received the stress recalled more negative photographs than neutral photographs than participants who were not stressed. In addition, participants in the stress group recalled a greater number of details from the negative photographs than the neutral photographs, whereas participants who were not stressed recalled fewer details from the negative photographs than from the neutral photographs. This finding suggests that stress during consolidation can improve the quality of memories in addition to increasing the amount of information remembered.

Despite the strong connection between emotional arousal and the effects of stress from the animal literature, some studies in humans have found that acute stress can enhance memory for neutral material (Beckner et al., 2006; Preuss & Wolf, 2009; Schwabe, Bohringer, et al., 2008). For example, Preuss & Wolf (2009) administered the Trier Social Stress Test (TSST), which involves giving a brief speech and completing a mental arithmetic task (Kirschbaum, Pirke, & Hellhammer, 1993), during consolidation. They found that participants in the stress group recalled more neutral images than participants in the control group, but the recall accuracy was the same for the emotional (both positive and negative) images for both groups.

Emotional content can be defined along two orthogonal dimensions: valence and arousal. Valence refers to how positive or negative a stimulus is, while arousal indicates the intensity of the emotional stimulus, ranging from calm to excitement (Lang, Greenwald, Bradley, & Hamm, 1993; Russell, 1980). Valence and arousal are orthogonal, because both positive and negative stimuli can be either highly arousing or not very arousing at all. As mentioned above, emotional materials are remembered more easily than neutral information, and this affect appears to be driven by arousal rather than valence (Dolcos, Denkova, & Dolcos, 2012; Dolcos, LaBar, & Cabeza, 2004a, 2004b). This memory benefit for emotionally arousing information is the result of enhanced activity in both the amygdala and the medial temporal lobe (MTL) memory system (Dolcos et al., 2012; Dolcos et al., 2004b; Kensinger & Corkin, 2004). In fact, memory for highly arousing emotional materials is superior to memory for less arousing, but still valenced, emotional materials (Dolcos et al., 2004b; Kensinger & Corkin, 2003). Although emotional arousal appears to be critical for the effects of stress on memory in

rodents, no human studies have directly manipulated the arousal level of the to-be-remembered stimuli. It is possible that more arousing stimuli are needed to see a selective effect of stress on memory for emotional materials in humans.

1.4 Current Study

The question of whether memory for neutral or emotional information is enhanced with stress during consolidation remains unanswered. It is possible that there are some circumstances in which stress during consolidation will lead to enhanced emotional memory and other that will lead to enhanced neutral memory. The goal of the current study was to determine under what circumstances memory for emotional material is improved following stress during consolidation. We suggested that memory for highly arousing negative material has the greatest likelihood of being enhanced by acute stress during consolidation. To investigate this, we had participants learn high arousal negative images, low arousal negative images, and neutral images. We administered a stressor to half the participants and a control task to the other half of participants immediately after encoding and assessed memory performance 48 hours later. In addition to recognition memory data, we also collected confidence ratings at retrieval to examine the quality of the retrieved memories. This has not been done in any previous stress and memory studies, and we wanted to see if stress affects confidence as well as accuracy. Based on previous research, we made the following predictions:

1. The stress group would have higher memory performance than the control group, especially for the high arousal negative images.
2. High arousal negative images would be remembered better than neutral images or low arousal negative images.

3. The high arousal negative images and the low arousal negative images would receive higher visual detail ratings than the neutral images.
4. Cortisol would increase in the stress group, but not in the control group. This increase in cortisol would be correlated with memory performance, with greater increases in cortisol corresponding to better memory performance.

CHAPTER 2

METHOD

2.1 Participants

The participants for this study were 78 young adult males. Participant demographics are in **Table 1**. There were 39 participants in the stress group and 39 participants in the control group. We only included male participants because of known sex differences in HPA axis functioning (Kajantie & Phillips, 2006; Kudielka & Kirschbaum, 2005). Cortisol increases more in men following stress than in women (Kudielka & Kirschbaum, 2005). Furthermore, menstrual phase and the use of oral contraceptives affect women's cortisol response, with greater cortisol increases in the luteal phase and lower cortisol increases with oral contraceptives (Kajantie & Phillips, 2006). Excluding female participants reduced the variability in the cortisol data and is consistent with previous studies that have only used male participants (Abercrombie et al., 2003; de Quervain et al., 2003; Khalili-Mahani, Dedovic, Engert, Pruessner, & Pruessner, 2010; Maheu et al., 2005; Maheu et al., 2004; Oei et al., 2007; Pruessner et al., 2008; Schwabe et al., 2009). Participants received either $10 per hour plus $5 per day for travel expenses or course credit as compensation. All participants received a $5 bonus for showing up for the second session. All participants signed consent forms approved by the Georgia Institute of Technology Institutional Review Board.

Table 1: Participant Demographics

	Age	Years of Education
Mean (SD)	20.31 (2.43)	14.14 (1.85)
Range	18 - 29	12 - 21

Note: Standard deviations in parentheses

Participants completed a health questionnaire before their first session to ensure that they did not have any medical conditions that could affect either the results of the study or the individual's ability to participate in the study. Potential participants who reported any of the following conditions were excluded from the study: Epilepsy, Parkinson's disease, a history of stroke or seizure, untreated depression, untreated anxiety, Attention Deficit Disorder, Multiple Sclerosis, uncontrolled hyper- or hypo-tension, untreated Diabetes, Sickle Cell Anemia, smoking or other regular use of nicotine, use of beta blockers, alcoholism, and regular use of illegal drugs. Participants were asked when they usually wake up in the morning, so that they would not be scheduled to participate within two hours of waking. Endogenous cortisol levels are highest at waking and then decline during the day. This decline is rapid in the morning and slower in the afternoon (Het, Ramlow, & Wolf, 2005; Maheu et al., 2005). Because we expected an acute increase in cortisol as a result of the stress manipulation, we wanted endogenous cortisol levels to be relatively low at the start of the experiment. For this reason, we ran all of the participants in the afternoon (1pm to 6pm).

In addition, participants completed the International Physical Activity Questionnaire Short Version, which assesses physical activity in the last week. At the beginning of each experimental session, participants were asked when they woke up that day, if they did any physical activity, and if they had any caffeine or nicotine. Participants who said they did some physical activity were asked what time they did that activity and for how long they did that activity. Participants who say they had caffeine or nicotine were asked when they had the caffeine or nicotine. Participants were informed that they are to refrain from physical exercise, caffeine, and nicotine within two hours of

an experimental session when they were scheduled. Participants who did not comply with these instructions were allowed to complete the study.

2.2 Materials

Stimuli consisted of 450 color photographs from the Nencki Affective Picture System (NAPS) and contained 150 high arousal negative images, 150 low arousal negative images, and 150 neutral images (Marchewka, Zurawski, Jednorog, & Grabowska, 2013). The NAPS images consisted of photographs grouped into 5 categories based on their content: animals, faces, landscapes, objects, and people. The average valence and arousal ratings for these images can be found in **Table 2**. Neutral images had higher valence ratings than the low arousal negative images [t (298) = 55.559, $p < .001$] and the high arousal negative images [t (298) = 31.977, $p < .001$]. The low arousal negative images and the high arousal negative images were matched for valence [t (298) = .580, $p = .563$]. The high arousal negative images had higher arousal ratings than the low arousal negative images [t (298) = 25.073, $p < .001$] and the neutral images [t (298) = 29.369, $p < .001$]. The low arousal negative images had higher arousal ratings than the neutral images [t (298) = 12.483, $p < .001$].

Table 2: NAPS Stimuli

	Valence	Arousal
Neutral	6.489 (.273)	4.547 (.745)
Low Arousal Negative	3.801 (.526)	5.416 (.414)
High Arousal Negative	3.747 (1.014)	6.503 (.333)

Note: Standard deviations in parentheses

Salivary cortisol levels were assessed using the Salimetrics Oral Swab (SOS) and were sent to Salimetrics for immunoassay. The collection and storage of saliva samples were done in accordance with the requirements for safe handling of biological materials from the Georgia Institute of Technology Environmental Health and Safety Office.

Salimetrics provided this information about the immunoassay procedure and reliability:

Saliva samples were assayed in duplicate to determine cortisol levels using a highly sensitive enzyme immunoassay (Salimetrics, State College, PA). The test used 25 µL of saliva per determination, has a lower limit of sensitivity of 0.007 µg/dL, standard curve range from 0.012 µg/dL to 3.0 µg/dL, an average intra-assay coefficient of variation of 4.6% and an average inter-assay coefficient of variation of 5.9%. Method accuracy determined by spike and recovery averaged 105.3% and linearity determined by serial dilution averaged 105.3%. Values from matched serum and saliva samples show the expected strong linear relationship, r (47) = 0.91, $p < .0001$.

2.3 Procedure

There were 2 lab sessions 48 hours apart. The use of this memory delay is consistent with the literature and ensured that the stress only occurs during consolidation and did not carry over into retrieval (for review, see Wolf, 2008). Participants were asked to refrain from caffeine and nicotine for the 2 hours prior to each session. All sessions took place in the afternoon (between 1pm and 6pm), so that basal cortisol levels were relatively low and stable (Het et al., 2005; Maheu et al., 2005).

2.3.1 Session 1

The first session lasted approximately 1.5 hours. Participants first completed a practice encoding task with 10 trials. The encoding task is depicted in **Figure 1**.

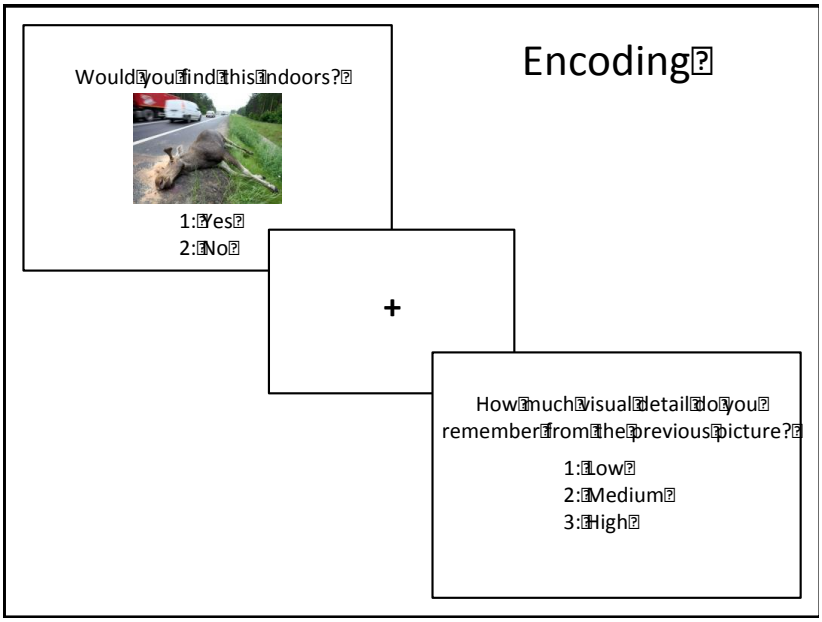


Figure 1: Encoding Procedure

The first saliva sample was collected immediately following the practice encoding task. The encoding task contained 75 low arousal negative images, 75 high arousal negative images, and 75 neutral images. There were 5 blocks, each with 15 low arousal negative images, 15 high arousal negative images, and 15 neutral images. First, participants saw each image for 3000 milliseconds in the center of the screen with the question "Would you find this indoors?" written above the image. Participants responded with "1" on the number pad for yes and "2" on the number pad for no. These response choices were displayed on the screen below the image. After the image disappeared, participants were asked how much visual detail they remembered from the image. Participants responded with "1" for low visual detail, "2" for medium visual detail, and "3" for high visual detail. These response choices were displayed in the center of the screen for 3000 milliseconds. Participants were not informed that their memory for these images would be tested.

We asked participants to report how much visual detail they remembered during encoding, because we wanted to be able to assess the quality of participants' memories at retrieval. Previous research has found that negative material is likely to be remember with greater detail than neutral material, both in the context of a stress manipulation (Cahill et al., 2003) and independent of any stress manipulation (Kensinger & Schacter, 2008).

We used the Montreal Imaging Stress Task (MIST) to induce acute psychological stress immediately following encoding (Dedovic et al., 2005). The user interface of the MIST is shown in **Figure 2.**

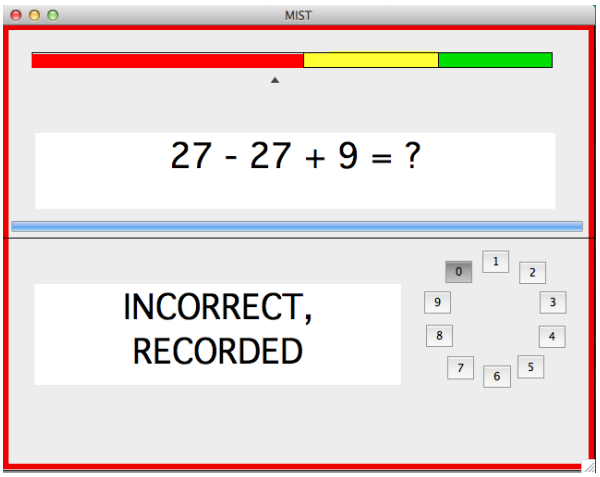


Figure 2: MIST User Interface

The MIST consists of mental arithmetic problems that participants in the stress condition must solve under a restrictive time limit and while receiving negative feedback about their performance. **Appendix A** contains a script with the negative feedback that was given to the participants in between runs. Participants in the control condition solved the same mental arithmetic problems but without a restrictive time limit and with no negative feedback. All participants completed three seven-minute runs of either the

control condition or the experimental condition of the MIST. The second saliva sample was collected immediately following the completion of the MIST.

2.3.2 Session 2

The second session lasted approximately an hour. Participants completed a practice retrieval task with 10 trials. The retrieval task is depicted in **Figure 3**.

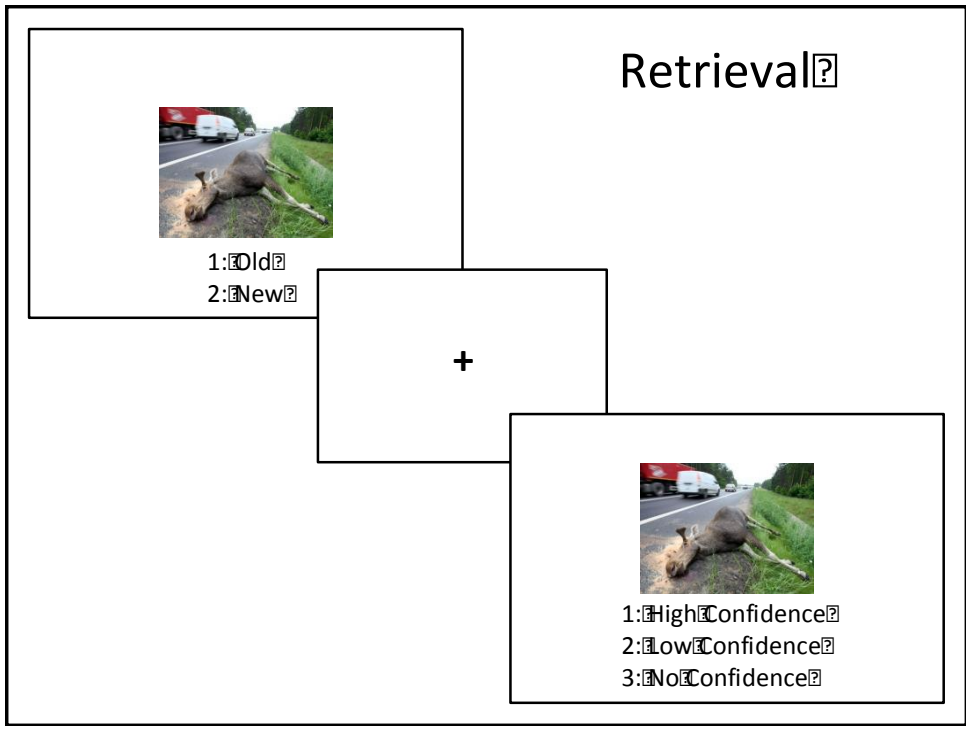


Figure 3: Retrieval Procedure

The retrieval task included the 225 images from the encoding task as well as 225 new images (75 low arousal negative, 75 high arousal negative, and 75 neutral). Retrieval was split into 10 blocks to avoid fatigue. Participants responded to 2 questions for each stimulus. First, participants viewed the image for 3000 milliseconds and indicated if the image was old or new. They responded with "1" for old and "2" for new on the number pad. Participants were instructed to respond "old" if they remembered seeing the image during the first session and "new" if they did not remember seeing the

image during the first session. Second, participants viewed the image for 3000 milliseconds and said how confident they were that the image was old or new. Participants responded with "1" for high confidence, "2" for low confidence, and "3" for no confidence. Participants were instructed to respond "high confidence" if they were completely sure of their response, "low confidence" if they were somewhat sure, but not completely sure of their response, and "no confidence" if they were just guessing. A fixation cross was displayed in the center of the screen for 500 milliseconds between each of these questions.

2.4 Data Analysis

2.4.1 Encoding Data

The visual detail data from the encoding task were analyzed by creating a visual detail score from the ratings given at encoding. For each item, high visual detail ratings were given a score of 3, medium visual detail ratings were given a score of 2, and low visual detail ratings were given a score of 1. The average visual detail scores for neutral images, low arousal negative images, and high arousal negative images were submitted to a 2 Group (stress, control) X 3 Category (neutral, low arousal negative, high arousal negative) ANOVA. We predicted an effect of Category, such that the high arousal negative images and the low arousal negative images would receive higher visual detail ratings than the neutral images. We did not predict an effect of group, because these ratings were provided before the stress manipulation.

2.4.2 Retrieval Data

We used the P_r discrimination index (hit rate – false alarm rate) to assess item memory performance (Snodgrass & Corwin, 1988). The item memory data were

submitted to a 2 Group (stress, control) X 3 Category (neutral, low arousal negative, high arousal negative) ANOVA. We predicted a main effect of Group, a main effect of Category, and a Group X Category interaction. For the main effect of Group, we compared item memory for the stress group and the control group, and we predicted that the stress group would have higher memory performance than the control group. For the main effect of Category, we compared item memory for neutral images, low arousal negative images, and high arousal negative images. We predicted that memory would be better for the high arousal negative images than both the low arousal negative images and the neutral images, with no difference in memory between the low arousal negative images and the neutral images. For the Group X Category interaction, we examined if the effect of stress on memory performance was the same for each of the arousal categories. We predicted that stress would improve memory for the high arousal negative images to a greater extent than for the low arousal negative images or the neutral images.

The confidence data were analyzed by creating a confidence score from the ratings given at retrieval. For each item, high confidence ratings were given a score of 3, low confidence ratings were given a score of 2, and no confidence ratings were given a score of 1. The average confidence scores were submitted to a 2 Group (stress, control) X 3 Category (neutral, low arousal negative, high arousal negative) ANOVA. We predicted a main effect of Group, with the stress group having overall higher confidence in their responses than the control group, and a main effect of Category, with the highest confidence given to the high arousal negative items. We also predicted a Group X Category interaction, with the greatest increase in confidence in the stress group for the high arousal negative items.

The recognition memory data were further analyzed according to the visual detail rating that was given at encoding. We calculated the hit rate for each visual detail rating given at encoding (i.e., of the images remembered with high visual detail at encoding, how many were hits at retrieval and so on for medium and low visual detail). These data were submitted to a 2 Group (stress, control) X 3 Category (neutral, low arousal negative, high arousal negative) X 3 Visual Detail (high, medium, low) ANOVA. We predicted a main effect of Visual Detail and predicted that items remembered with high visual detail at encoding would be more likely to be remembered at encoding than items remembered with medium or low visual detail.

2.4.3 Cortisol Data

The cortisol data were analyzed using a raw difference score that indicated the change in cortisol following the MIST. These data were submitted to an independent sample t-test, which compared the change in cortisol from the stress group to the change in cortisol from the control group. We predicted that cortisol level would increase in the stress group, but not in the control group. Because other studies using the MIST have found cortisol responders and non-responders in the stress group (Dedovic et al., 2005; Pruessner et al., 2008; Pruessner et al., 2010), we divided our stress group in to responders, those who had an increase in cortisol (i.e., any change above zero) following the MIST, and non-responders, those who did not have an increase in cortisol.

We further analyzed the retrieval data using three groups: responders, non-responders, and controls to examine the influence of cortisol response on memory performance. Item memory was analyzed using Pr and these data were submitted to a 3 Group (responder, non-responder, control) X 3 Category (neutral, low arousal negative,

high arousal negative) ANOVA. We predicted a main effect of group, with higher memory performance in the responders than the non-responders and the control participants. We also predicted a main effect of Category, with better memory for high arousal negative items than for low arousal negative items and neutral items. We also predicted a Group X Category interaction, with the best memory for the high arousal negative in the responders.

We analyzed the confidence data with a 3 Group (responder, non-responder, control) X 3 Category (neutral, low arousal negative, high arousal negative) ANOVA. We predicted a main effect of Group, with the responders having higher confidence than the non-responders and the controls. We predicted a main effect of Category with higher confidence for the high arousal negative items than the low arousal negative items and the neutral items. We also predicted a Group X Category interaction, with the greatest increase in confidence in the responders for the high arousal negative items.

We also correlated the change in cortisol with item memory performance, confidence ratings for hits, and hit rate based on the visual detail ratings provided at encoding. We predicted a positive correlation between change in cortisol and all three measure, meaning that greater increases in cortisol would lead to better memory and higher confidence.

2.4.4 Time of Day Analysis

We ran all of the participants in the afternoon because of the known circadian rhythm of endogenous cortisol levels (Het et al., 2005; Maheu et al., 2005). However, these endogenous changes occur based on when the individual wakes up rather than the absolute time of day. Because people wake up at different times in the morning, we

wanted to check that the participants in the different groups (responders, non-responders, and controls) had not been awake for different amounts of time when they came in for the first session. To do this, we calculated how long each participant had been awake by subtracting the time they woke up from the time session 1 began. Then we ran a one-way ANOVA on the responders, the non-responders, and the control participants to determine if there were any differences in how long they had been awake. We predicted that we would not find any differences in how long the participants had been awake across any of the groups.

CHAPTER 3

RESULTS

We used the Hyunh-Feldt correction when sphericity could not be assumed. This is reflected in the degrees of freedom and the *p*-values.

3.1 Encoding

We analyzed the visual detail ratings from encoding to determine how much visual detail participants reported remembering for each stimulus category. We averaged the ratings participants provided for each stimulus category. The visual detail data from encoding are displayed in **Figure 4**.

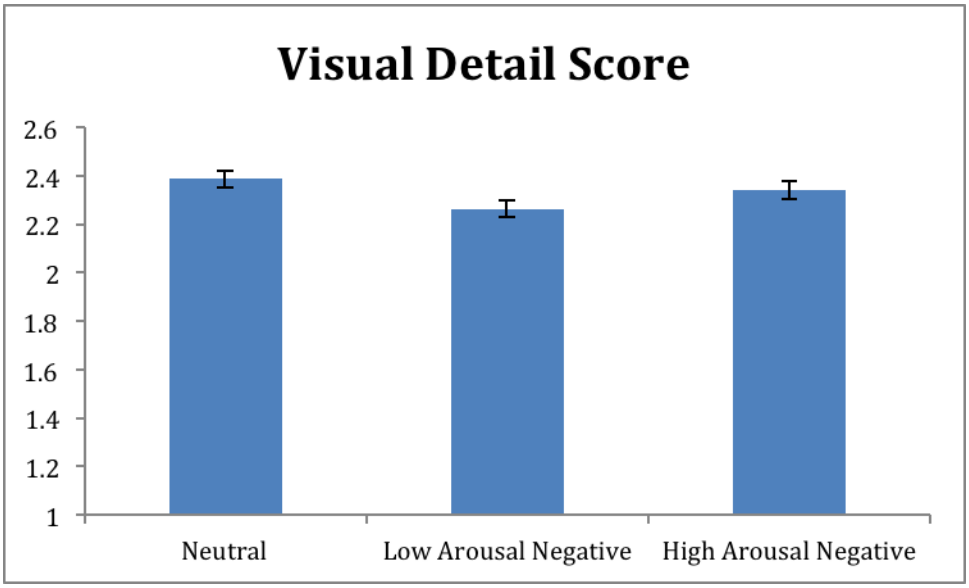


Figure 4: Encoding Data

These data were submitted to a 2 Group (stress, control) X 3 Category (neutral, low arousal negative, high arousal negative) ANOVA. There was no main effect of Group [F (1, 76) < 1, η^2 = .008], so we collapsed across groups. We then submitted the data to a repeated measures ANOVA to compare the visual detail ratings participants provided for each stimulus category across groups. There was a main effect of Category

[F (2, 152) = 28.064, p < .001, η^2 = .271]. Follow-up t-tests indicated that participants reported remembering more visual details from neutral images than from low arousal negative images [t (77) = 7.659, p < .001] and high arousal negative images [t (77) = 2.437, p = .017]. Participants also reported remembering more visual details from high arousal negative images than from low arousal negative images [t (77) = 5.137, p < .001].

3.2 Retrieval

3.2.1 Item Memory

We analyzed item memory performance to determine the effect of stress on subsequent memory performance. We used the Pr discrimination index (hit rate – false alarm rate) to assess item memory performance (Snodgrass & Corwin, 1988). The item memory data are displayed in **Figure 5** and the hit and false alarm rates for each group are in **Table 3**.

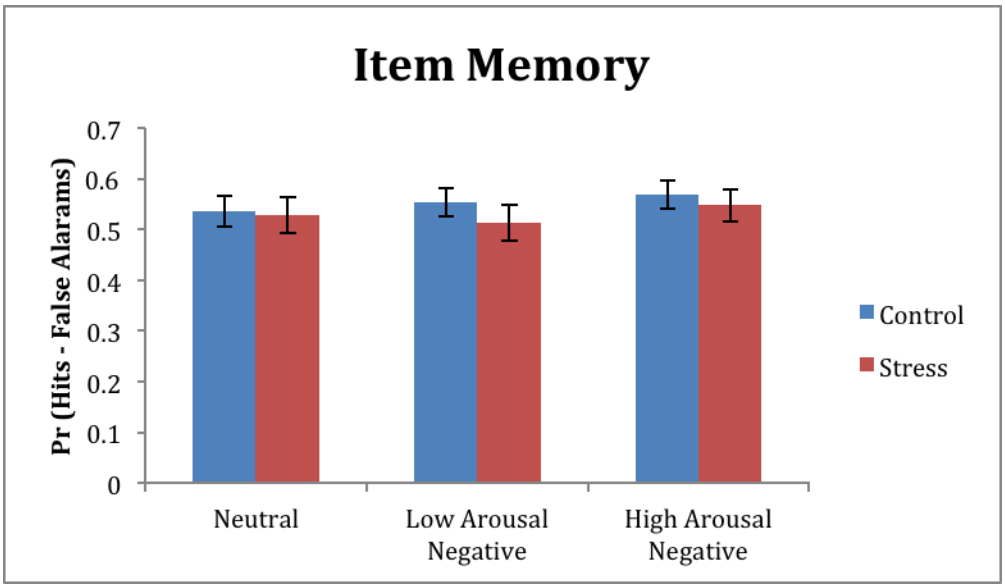


Figure 5: Item Memory Data

The data were submitted to a 2 Group (stress, control) X 3 Category (neutral, low arousal negative, high arousal negative) ANOVA. There was a main effect of Category

[F (2, 152) = 3.356, p = .037, η^2 = .042] and no main effect of Group [F (1, 76) < 1, η^2 = .004]. There was no Category X Group interaction [F (2, 152) < 1, η^2 = .012]. Follow-up t-tests on the main effect of Category indicated that memory was better for high arousal negative images than both low arousal negative images [t (77) = 2.134, p = .036] and neutral images [t (77) = 2.255, p = .027]. There was no difference in memory between low arousal negative images and neutral images [t (77) < 1].

Table 3: Item Memory Accuracy

a) Control Group

	Neutral	Low Arousal	High Arousal
Hit Rate	.721 (.175)	.750 (.162)	.790 (.150)
False Alarm Rate	.186 (.134)	.198 (.130)	.220 (.124)
Pr (Hit Rate – False Alarm Rate)	.535 (.190)	.552 (.175)	.569 (.176)

Note: Standard deviations in parentheses

b) Stress Group

	Neutral	Low Arousal	High Arousal
Hit Rate	.692 (.190)	.695 (.168)	.746 (.152)
False Alarm Rate	.164 (.103)	.182 (.133)	.198 (.134)
Pr (Hit Rate – False Alarm Rate)	.528 (.223)	.513 (.218)	.548 (.195)

Note: Standard deviations in parentheses

3.2.2 Confidence

We analyzed the participants' confidence ratings to examine how confident participants were at retrieval. We averaged the participants' confidence ratings to create a confidence score. A response of "no confidence" was a 1, a response of "low confidence" was a 2, and a response of "high confidence" was a 3. The confidence data for hits are displayed in **Figure 6**. These data were submitted to a 2 Group (stress, control) X 3 Category (neutral, low arousal negative, high arousal negative) ANOVA.

There was a marginal main effect of Category [F (2, 152) = 2.710, p = .070, η^2 = .034]. There was a main effect of Group [F (1, 76) = 5.050, p < .028, η^2 = .062], indicating that the control group had higher confidence than the stress group for hits. There was no Category X Group interaction [F (2, 152 < 1, η^2 = .012]. Follow-up t-tests for the marginal main effect of Category indicated that participants rated their confidence as higher for hits to the high arousal negative images than hits to the low arousal negative images [t (77) = 2.306, p = .024]. There were no differences in the confidence ratings for hits to high arousal negative images and hits to neutral images [t (77) = 1.120, p = .266]. There were also no differences in the confidence ratings for hits to neutral images and hits to low arousal negative images [t (77) = 1.212, p = .229].

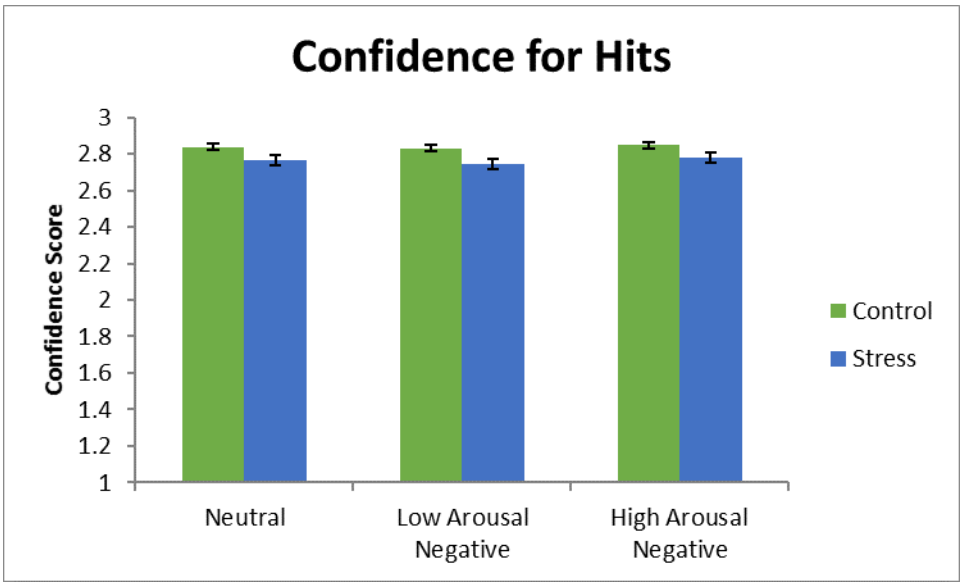


Figure 6: Confidence for Hits

We also analyzed the confidence ratings for misses in the same way that we analyzed the confidence ratings for hits. The confidence data for misses are in **Figure 7**. The confidence data for misses were submitted to a 2 Group (stress, control) X 3 Category (neutral, low arousal negative, high arousal negative) ANOVA. There was no

main effect of Category [F (1.866, 139.982) < 1, η^2 = .006], no main effect of Group [F (1, 75) = 1.671, p = .200, η^2 = .022], and no Category X Group interaction [F (1.866, 139.982) < 1, η^2 = .006].

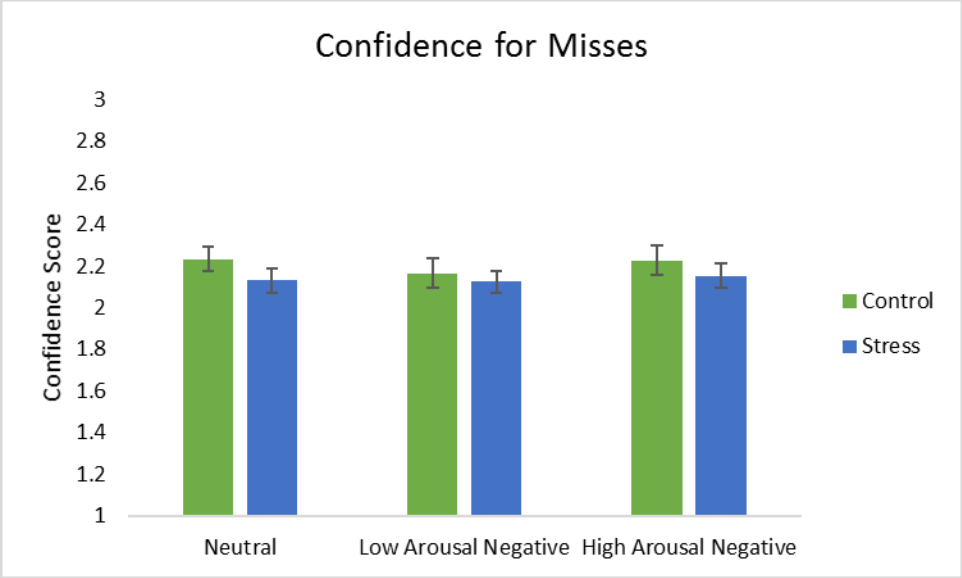
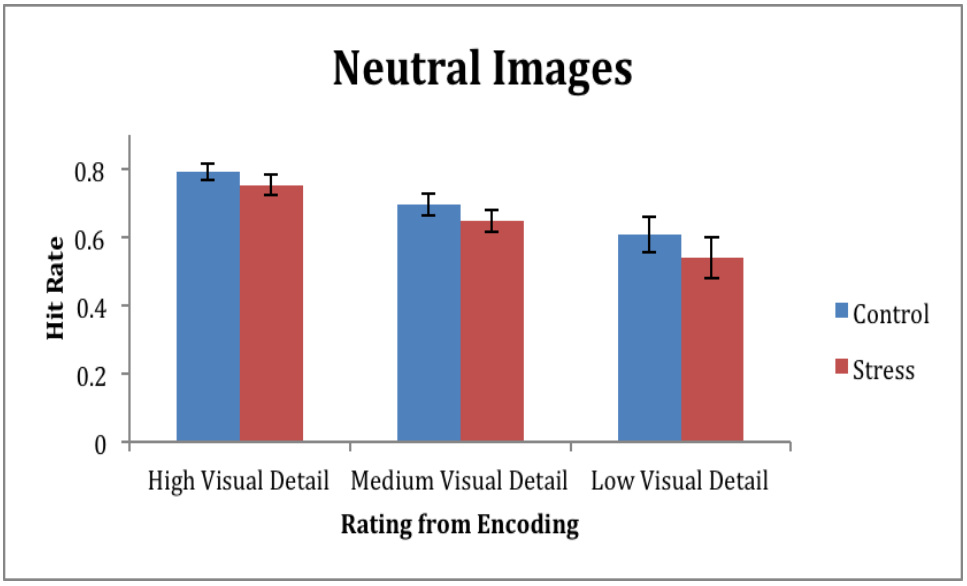


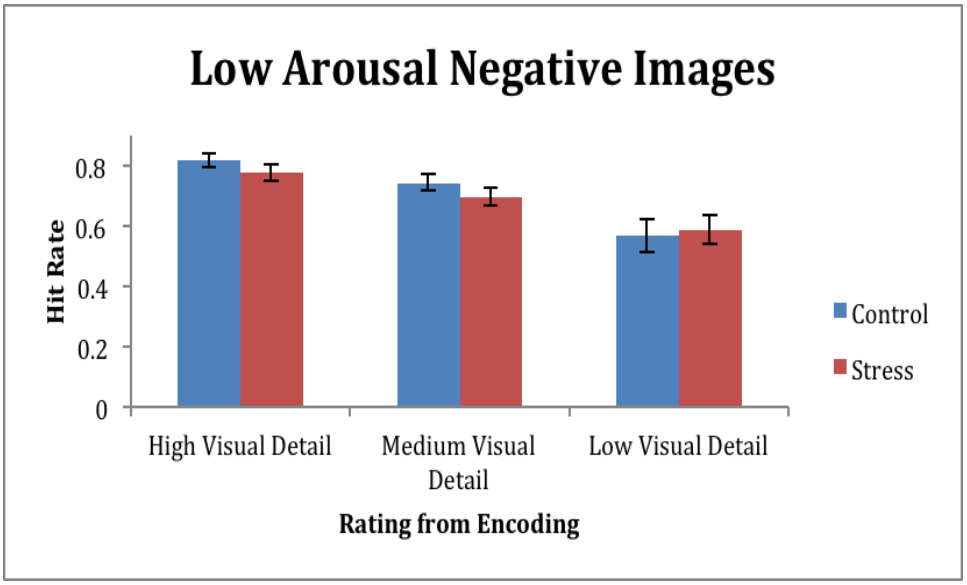
Figure 7: Confidence for Misses

3.2.3 Visual Detail

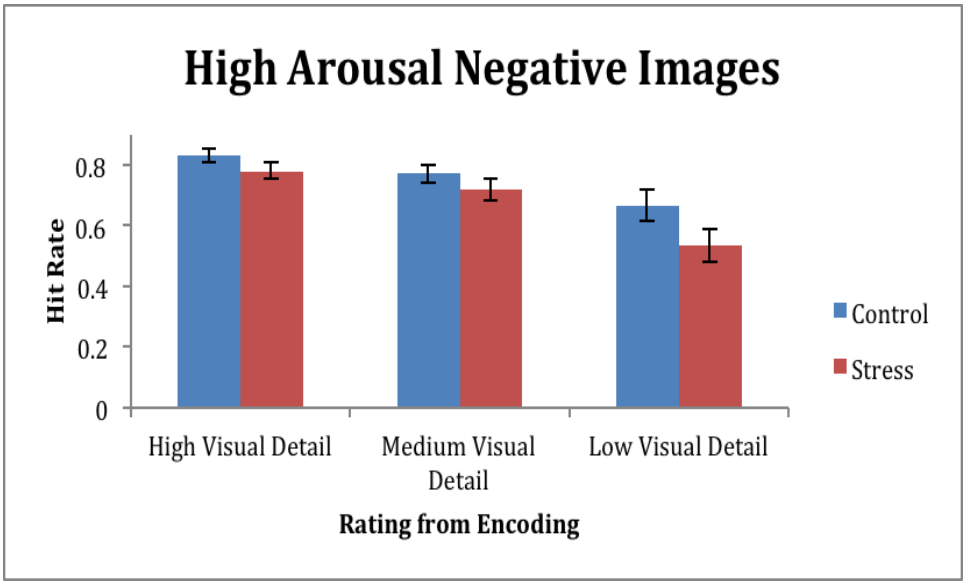
In order to determine the influence of rated visual detail on subsequent memory performance, we analyzed the hit rate based on the visual detail ratings given at encoding. We used the hit rate for this analysis, because we only have visual detail ratings for items that were presented at encoding. Therefore, we could not subtract false alarms with the same visual detail ratings from the hits. The data from this analysis are displayed in **Figure 8**. These data were submitted to a 2 Group (stress, control) X 3 Category (neutral, low arousal negative, high arousal negative) X 3 Visual Detail (high, medium, low) ANOVA. There was a main effect of Category [F (1.762, 133.925) = 3.828, p = .029, η^2 = .048] and a main effect of Visual Detail [F (1.260, 95.766) = 36.923, p < .001, η^2 = .327]. All other effects were not significant [F's < 1.88, p's > .174, η^2's < .024].



a) Neutral Images



b) Low Arousal Negative Images



c) High Arousal Negative Images

Figure 8: Visual Detail at Retrieval

Follow-up t-tests for the main effect of Category indicated that participants made fewer hits to neutral items than high arousal negative items [t (77) = 2.378, p = .020] and marginally fewer hits than low arousal negative items [t (77) = 1.921, p = .058]. Participants' hit rates for high arousal negative items and low arousal negative items were not different [t (77) = 1.209, p = .230]. Follow-up t-tests for the main effect of Visual Detail indicated that participants were more likely to remember items at retrieval that they reported remembering with high visual detail at encoding than items they reported remembering with medium visual detail at encoding [t (77) = 6.870, p < .001]. Participants were also more likely to remember items at retrieval that they reported remembering with medium visual detail at encoding than items they reported remembering with low visual detail at encoding [t (77) = 4.705, p < .001].

3.3 Cortisol

3.3.1 Change in Cortisol Analyses

We measured the change in cortisol following the MIST using a difference score (Pre-MIST – Post-MIST). The average change in cortisol for each group is displayed in **Figure 9,** and the change in cortisol for each subject is shown in **Figure 10.**

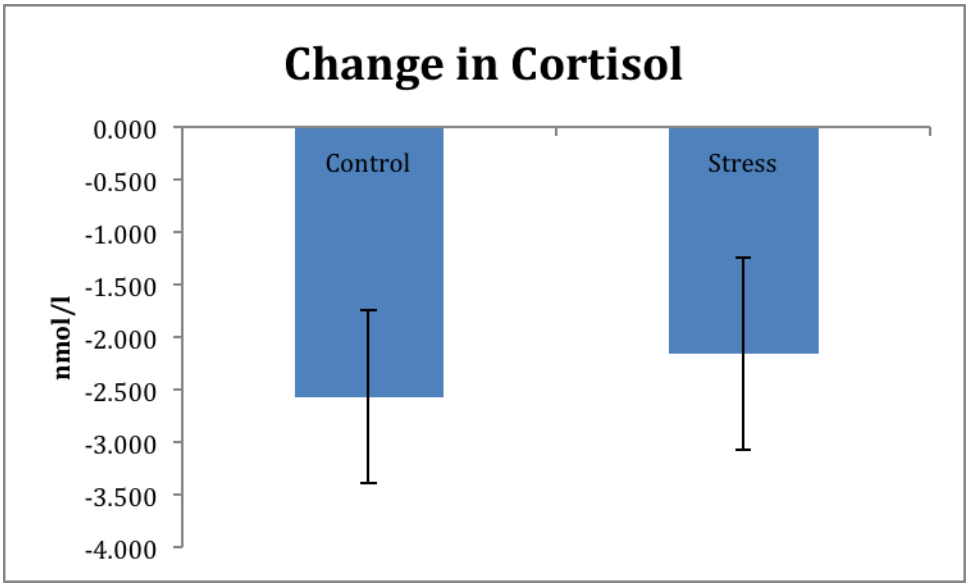


Figure 9: Average Change in Cortisol

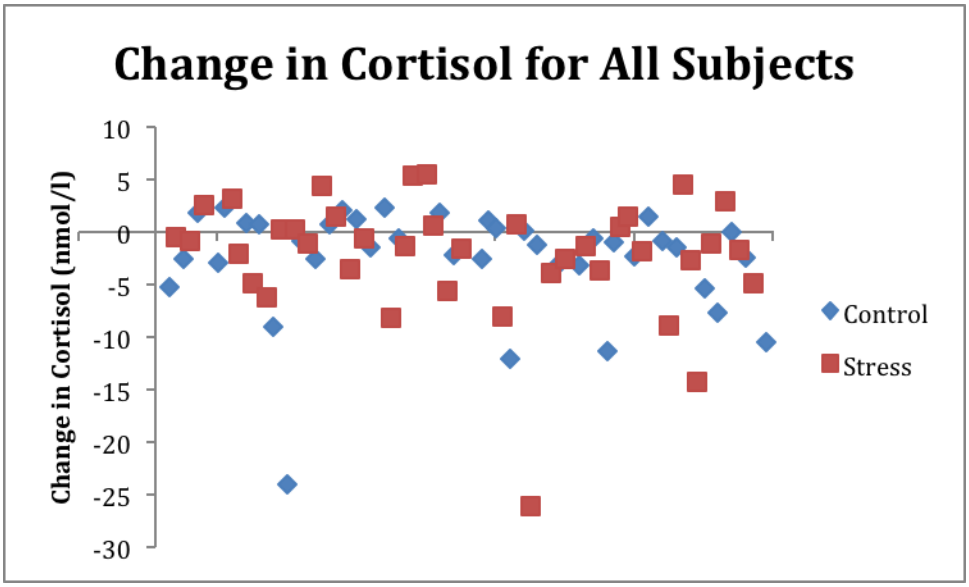


Figure 10: Change in Cortisol for All Subjects

The difference scores were submitted to an independent samples t-test. The change in cortisol following the MIST was not different in the stress group compared to the control group [t (76) < 1]. The change in cortisol was significantly less than zero for both the control group [t (38) = 3.125, p = .003] and the stress group [t (38) = 2.359, p = .024]. We then separated the stress group into responders and non-responders. Responders were participants who had an increase in cortisol following the MIST, and non-responders were participants who had a decrease in cortisol following the MIST. There were 14 responders and 25 non-responders. The average change in cortisol for responders and non-responders is displayed in **Figure 11,** and the change in cortisol for each subject in the stress group is shown in **Figure 12.** The change in cortisol in the responders was greater than the change in cortisol in the non-responders [t (37) = 4.617, p < .001]. The change in cortisol in the responders was significantly greater than zero [t (13) = 4.639, p < .001], while the change in cortisol in the non-responders was significantly less than zero [t (24) = 4.245, p < .001].

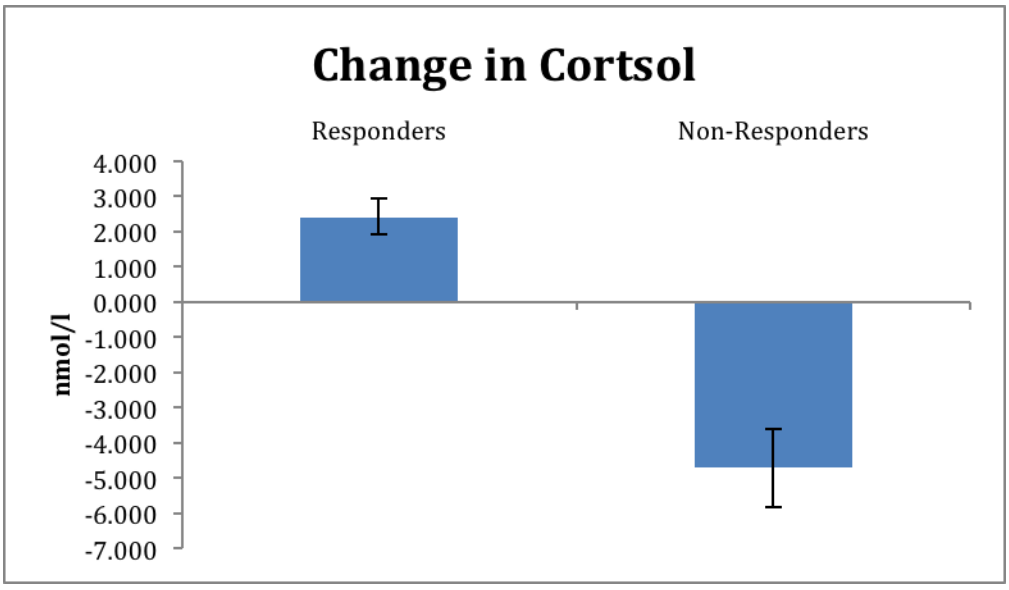


Figure 11: Average Change in Cortisol in the Stress Group

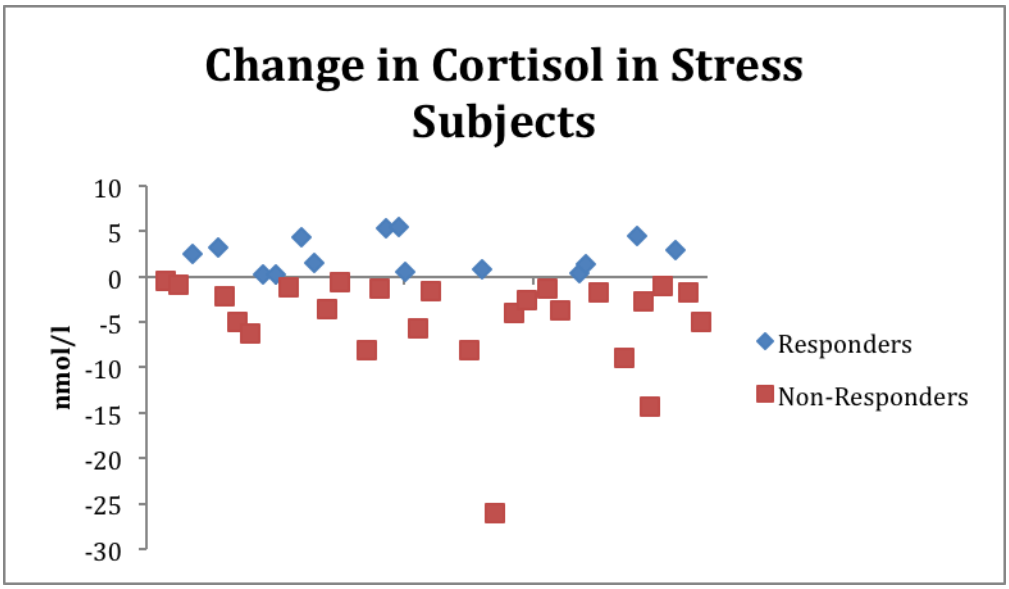


Figure 12: Change in Cortisol in Stress Subjects

3.3.2 Cortisol Response and Memory

We wanted to see if there were differences in memory performance between the cortisol responders, the cortisol non-responders, and the control participants. We first analyzed item memory performance with a 3 Group (responder, non-responder, control) X 3 Category (neutral, low arousal negative, high arousal negative) ANOVA. These data are in **Figure 13**. There was a marginal main effect of Category [F (2, 150) = 2.900, p = .058, η^2 = .037]. There was no main effect of Group [F (1, 75) < 1, η^2 = .016] and no Group X Category interaction [F (4, 150) < 1, η^2 = .013]. Follow-up t-tests for the marginal main effect of Category indicated that participants had better memory for the high arousal negative images than both the neutral images [t (77) = 2.255, p = .027] and the low arousal negative images [t (77) = 2.134, p = .036]. There was no difference in memory between the neutral images and the low arousal negative images [t (77) < 1].

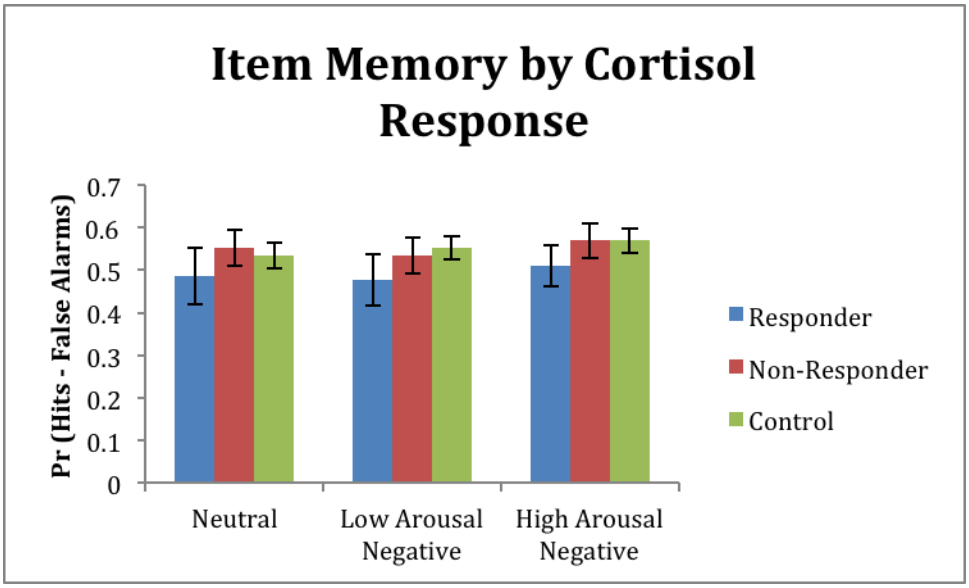


Figure 13: Item Memory by Cortisol Response

We then analyzed participants' confidence ratings for hits with a 3 Group (responder, non-responder, control) X 3 Category (neutral, low arousal negative, high arousal negative) ANOVA. These data are in **Figure 14.** There was a main effect of Category [F (2, 150) = 3.178, p = .045, η^2 = .041] and a main effect of Group [F (2, 75) = 5.382, p = .007, η^2 = .126]. There was no Group X Category interaction [F (4, 150) < 1, η^2 = .014]. Follow-up t-tests for the main effect of Category indicated that participants reported having higher confidence for hits to high arousal negative items than for hits to low arousal negative items [t (77) = 2.306, p = .024]. There were no differences in confidence between hits to the neutral items and hits to the low arousal negative items [t (77) = 1.212, p = .229] or hits to the high arousal negative items [t (77) = 1.120, p = .266]. Follow-up t-tests for the main effect of Group indicated that responders had lower confidence for hits than both control participants [t (51) = 3.135, p = .003] and non-responders [t (37) = 1.991, p = .054]. There was no difference in confidence for hits between the non-responders and the control participants [t (62) = 1.138, p = .003].

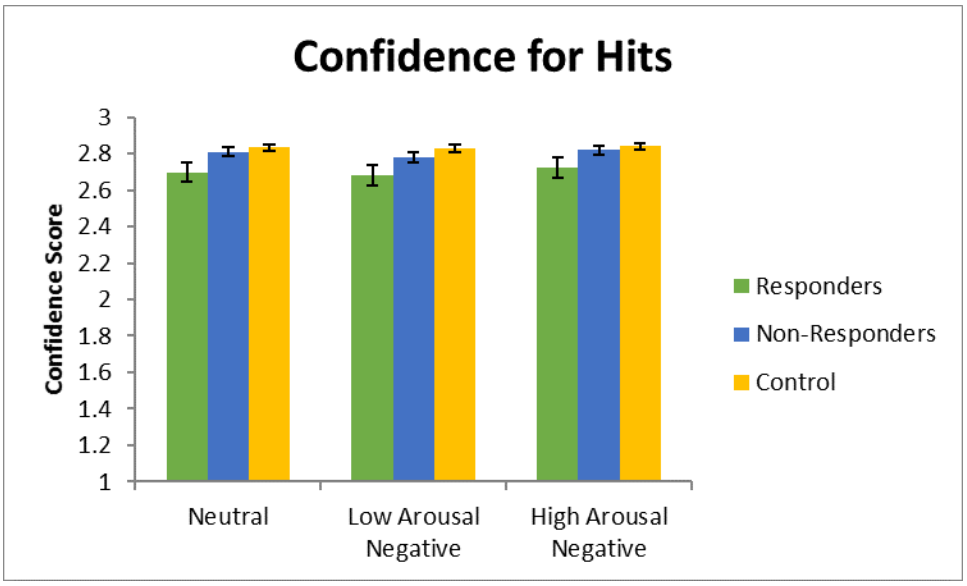


Figure 14: Confidence for Hits by Cortisol Response

We analyzed participants' confidence ratings for misses with a 3 Group (responder, non-responder, control) X 3 Category (neutral, low arousal negative, high arousal negative) ANOVA. These data are in **Figure 15**. There was no main effect of Category [F (1.889, 139.812) < 1, η^2 = .004], no main effect of Group [F (1, 74) = 1.439, p = .244, η^2 = .037], and no Category X Group interaction [F (3.779, 139.812) < 1, η^2 = .014].

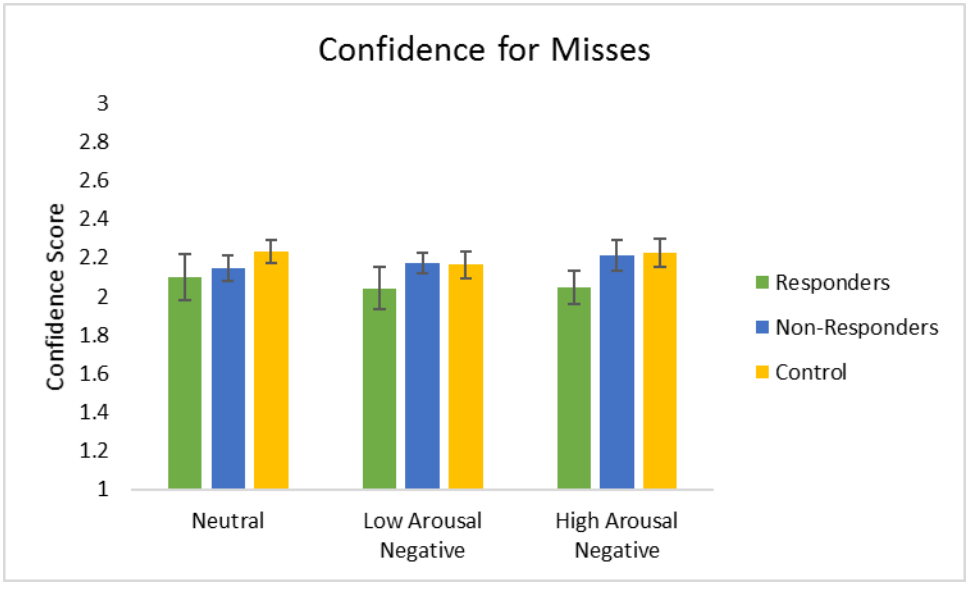
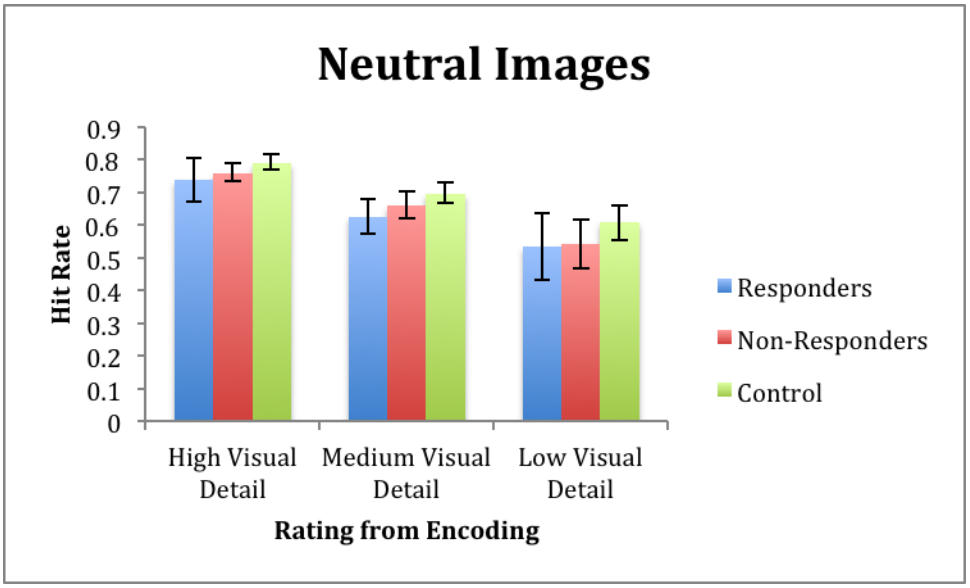
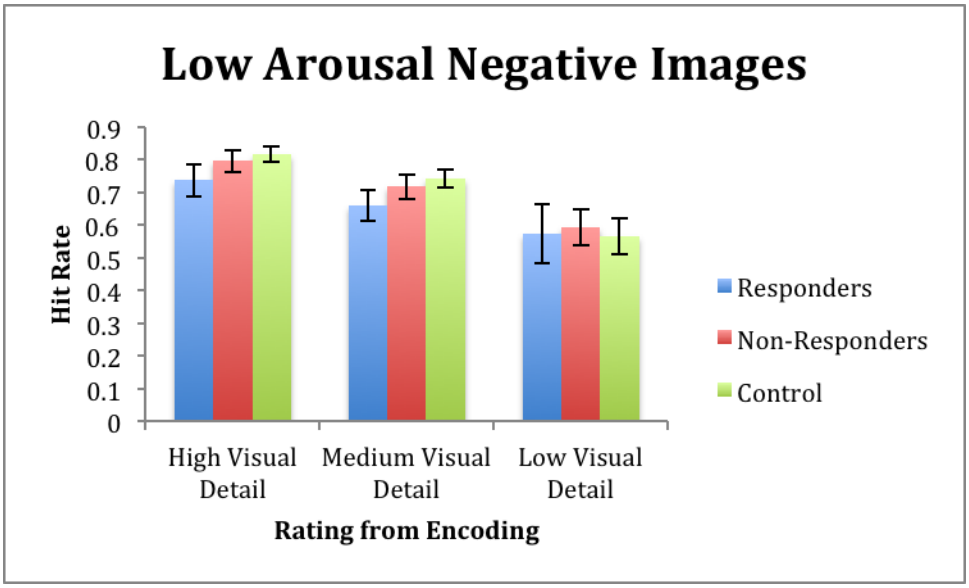


Figure 15: Confidence for Misses by Cortisol Response

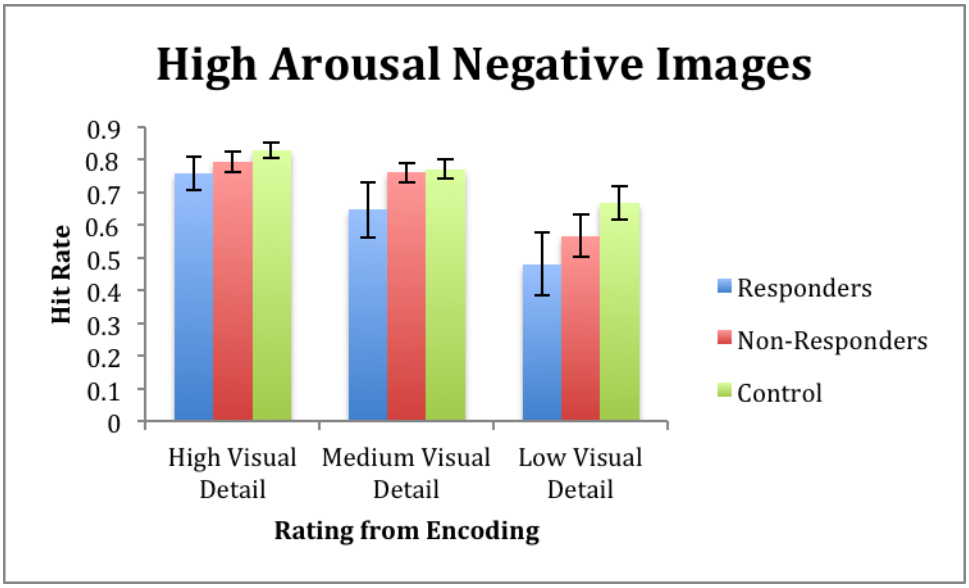
Third, we analyzed whether the visual detail ratings given at encoding affected subsequent memory performance in the responders, the non-responders, and the control participants with a 3 Group (responder, non-responder, control) X 3 Category (neutral, low arousal negative, high arousal negative) X 3 Visual Detail (high, medium, low) ANOVA. These data are in **Figure 16**. There was a main effect of Visual Detail [F (1.274, 95.574) = 31.404, $p < .001$, $\eta^2 = .295$]. None of the other effects in this analysis were significant [all F's < 2.168, all p's > .124, η^2's < .034]. Follow-up t-tests for the main effect of Visual Detail indicated that participants were more likely to remember items that they reported remembering with high visual detail at encoding than items that they reported remembering with medium visual detail at encoding [t (77) = 6.870, $p <$ .001]. Participants were also more likely to remember items that they reported remembering with medium visual detail at encoding than items that they reported remembering with low visual detail at encoding [t (77) = 4.705 $p < .001$].



a) Neutral Images



b) Low Arousal Negative Images



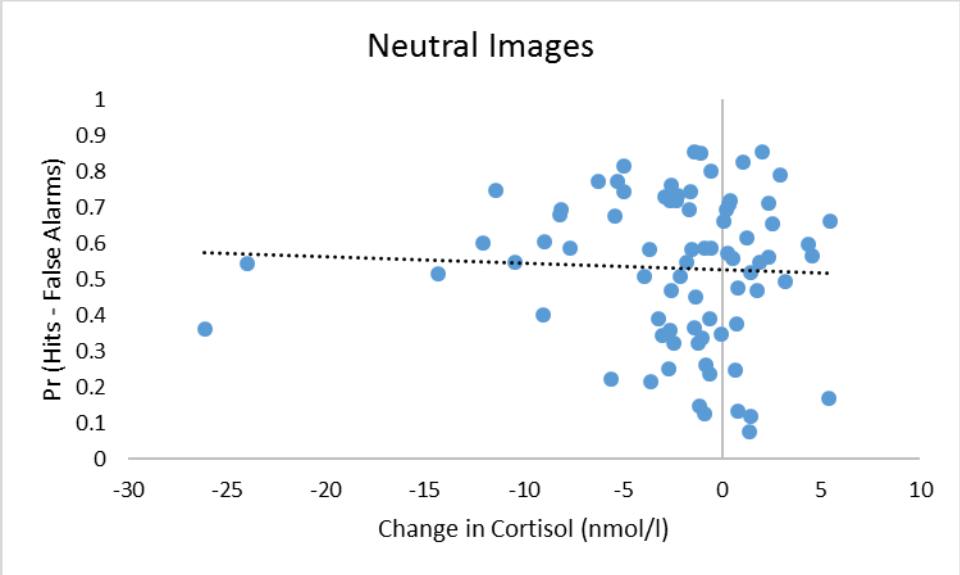
c) High Arousal Negative Images

Figure 16: Visual Detail by Cortisol Response

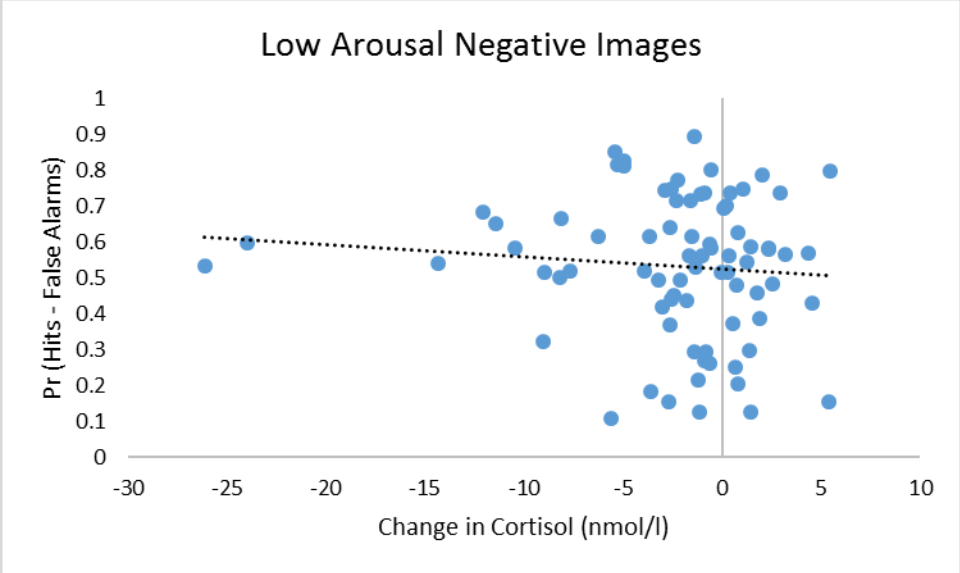
3.3.3 Correlational Analyses

We correlated the change in cortisol with item memory performance across responders, non-responders, and control participants. These data are displayed in **Figure 17**. There was no significant correlation between cortisol and item memory performance

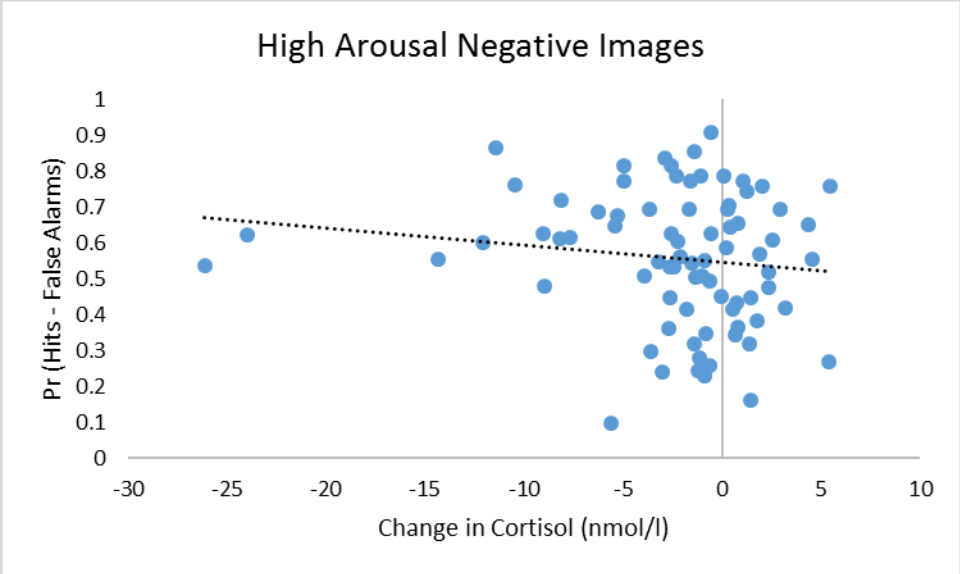
for neutral images [r = -.047, r^2 = .002, p = .684], low arousal negative images [r = -.094, r^2 = .009, p = .413], high arousal negative images [r = -.139, r^2 = .019, p = .227], or all images [r = -.096, r^2 = .009, p = .403].



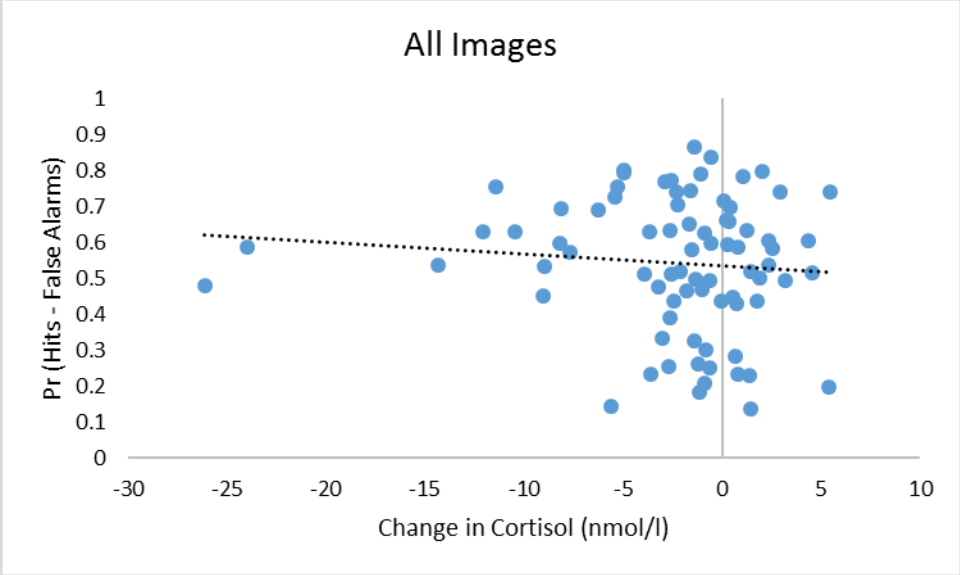
a) Neutral Images



b) Low Arousal Negative Images



c) High Arousal Negative Images

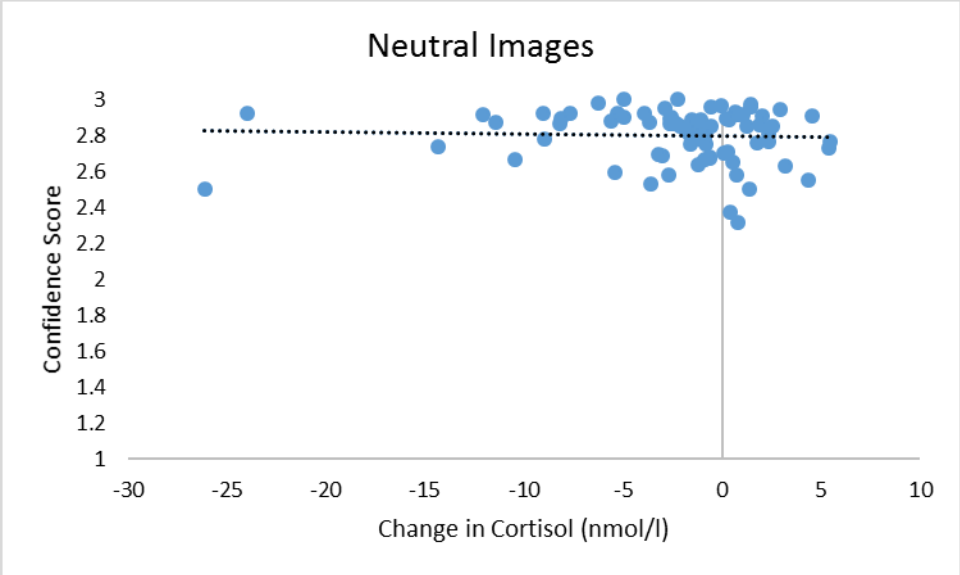


d) All Images

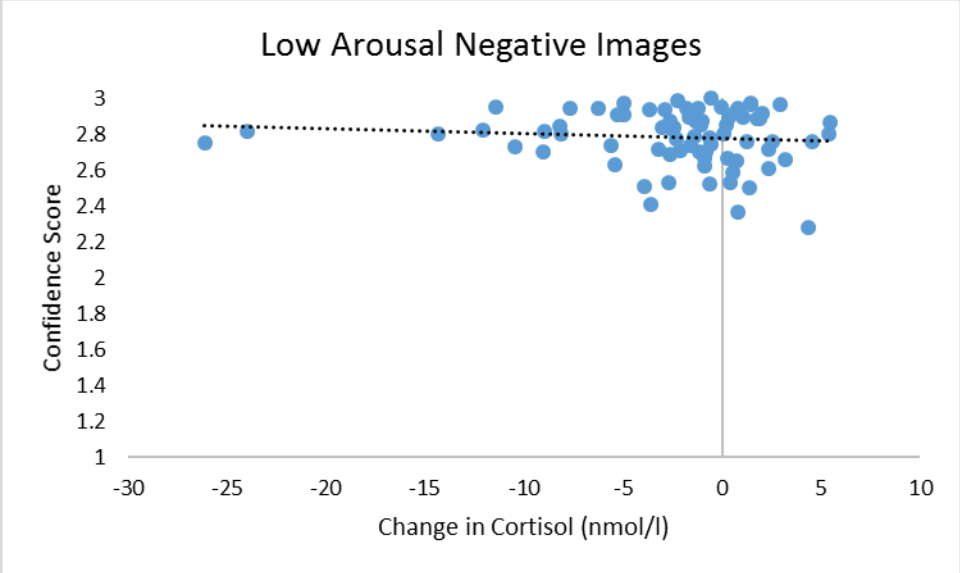
Figure 17: Cortisol-Item Memory Correlations

We then correlated the change in cortisol with the average confidence ratings for hits. These data are shown in **Figure 18**. There was no significant correlation between

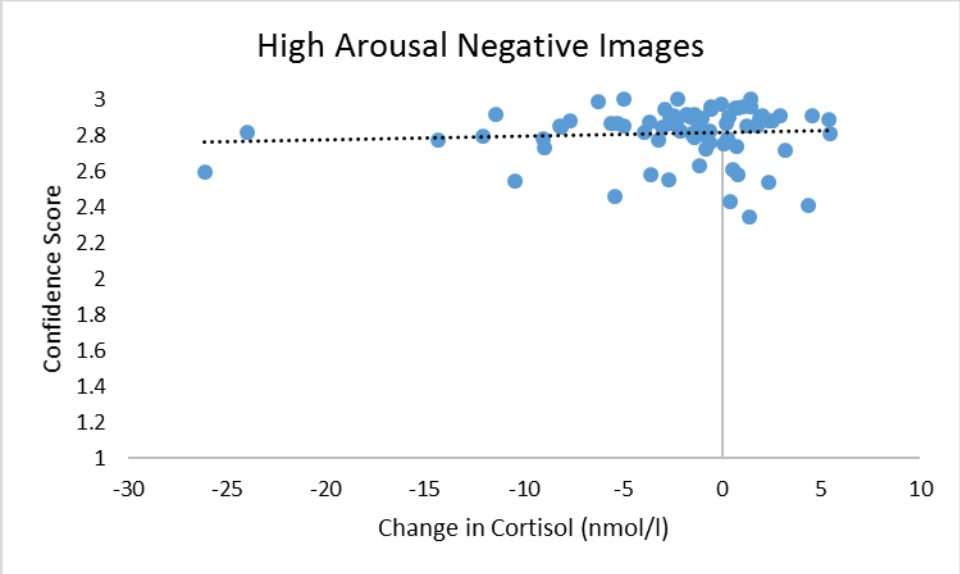
change in cortisol and confidence for hits for neutral images [r = -.042, r^2 = .002, p = .713], low arousal negative images [r = -.094, r^2 = .009, p = .413], high arousal negative images [r = .082, r^2 = .007, p = .475], or all images [r = -.021, r^2 = .004, p = .853].



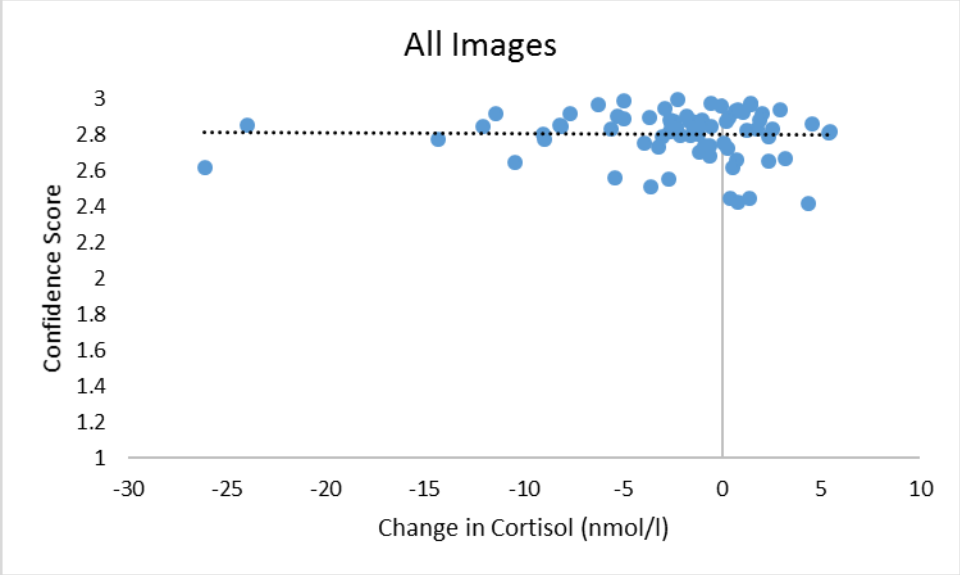
a) Neutral Images



b) Low Arousal Negative Images



c) High Arousal Negative Images

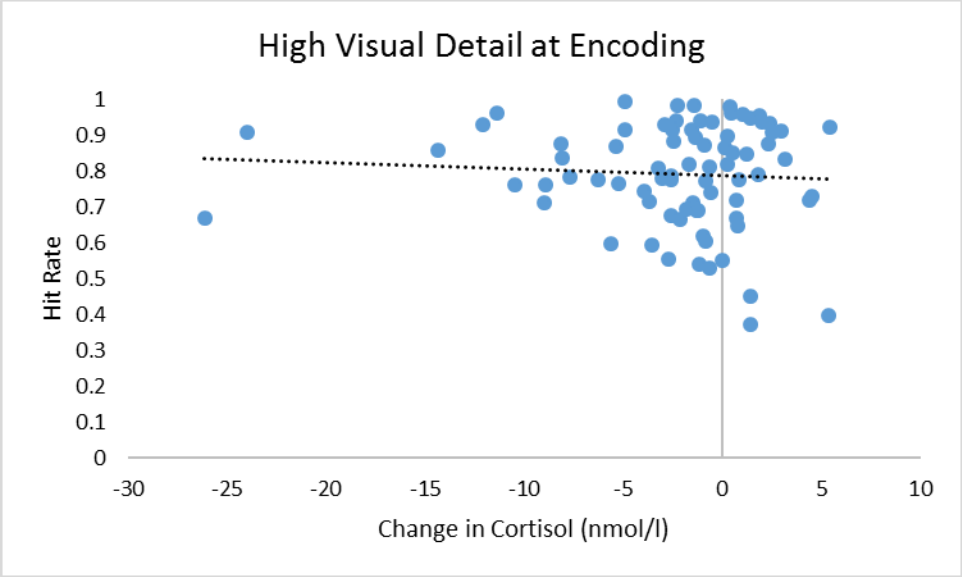


d) All Images

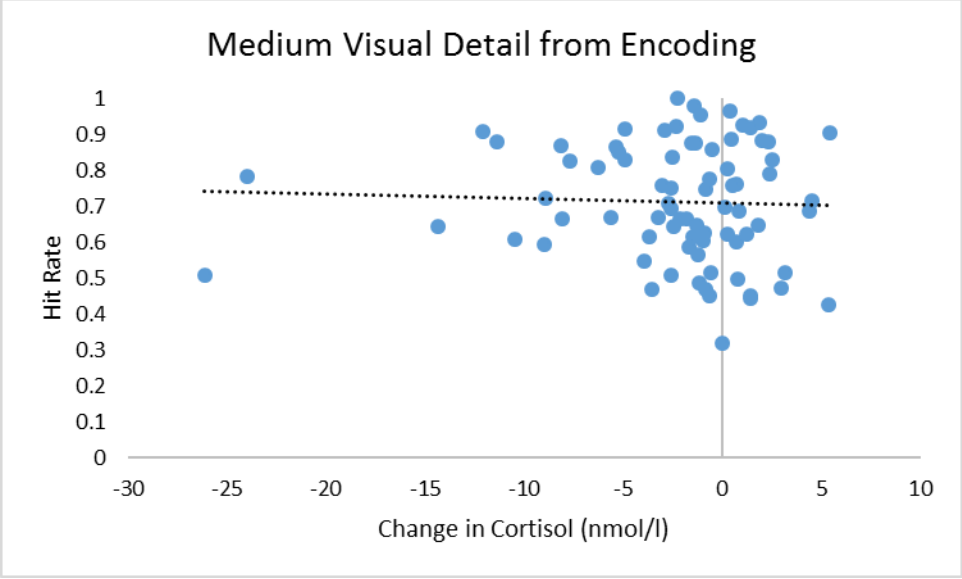
Figure 18: Cortisol-Confidence Correlations

We finally correlated the change in cortisol with the hit rate based on the visual detail ratings given at encoding. These data are shown in **Figure 19**. There was no

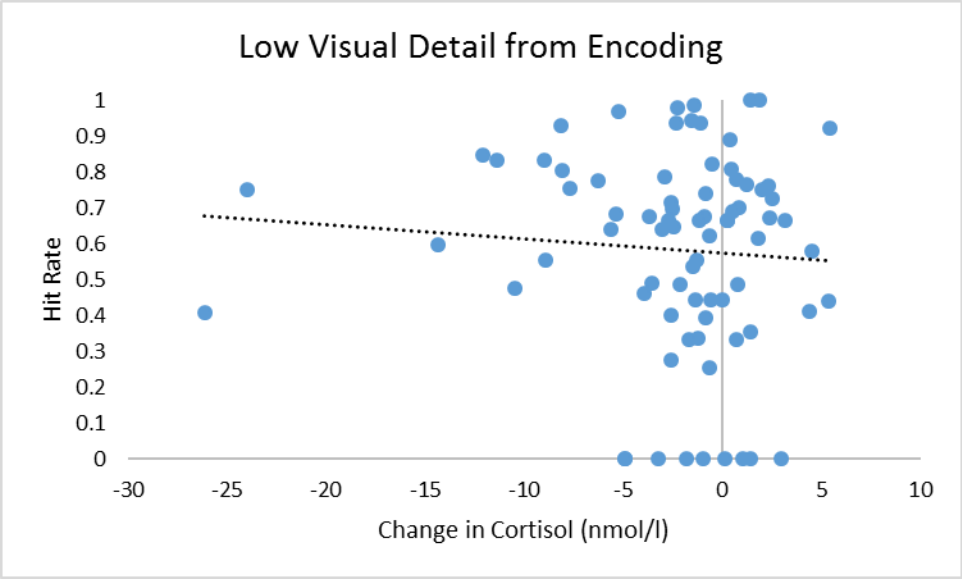
significant correlation between change in cortisol and images that participants reported remembering with high visual detail at encoding [r = -.071, r^2 = .005, p = .535], images that participants reported remembering with medium visual detail at encoding [r = -.039, r^2 = .002, p = .737], or images that participants reported remembering with low visual detail at encoding [r = -.077, r^2 = .006, p = .503].



a) High Visual Detail



b) Medium Visual Detail



c) Low Visual Detail

Figure 19: Cortisol-Visual Detail Correlations

3.4 Time Awake

At the beginning of session 1, participants were asked what time they woke up that morning. We calculated how long the participants had been awake by subtracting the time they woke up from the time session 1 began. These data are in **Table 4**. We ran a one-way ANOVA on the responders, the non-responders, and the control participants to determine if there were any differences in how long they had been awake when they came in for the first session. There was no main effect of Group [F (2, 77) < 1], therefore there was no difference in how long participants had been awake across the responders, the non-responders, and the control participants.

Table 4: Time Awake

	Hours Awake
Responders	5.91 (1.82)
Non-Responders	5.90 (2.60)
Control	6.48 (1.86)

Note: Standard deviations in parentheses

CHAPTER 4

DISCUSSION

We decided to conduct this study, because we wanted to investigate whether acute psychological stress during consolidation (immediately following encoding) enhances memory for highly arousing negative pictures. Previous research has demonstrated that stress during consolidation improves later memory performance in human participants (Beckner et al., 2006; Cahill et al., 2003; Preuss & Wolf, 2009; Smeets et al., 2008). Animal research also indicates that acute stress and elevated levels of glucocorticoids during consolidation enhance memory in rodents (Roozendaal, 2002). Evidence from animal studies shows that the early consolidation period immediately following encoding is the critical time for these effects, as injections of glucocorticoids improve memory only when administering immediately after training and do not improve memory when administered several hours later (Flood et al., 1978; Kovacs et al., 1977; Roozendaal & McGaugh, 1996; Roozendaal et al., 1999). The beneficial effect of acute stress during consolidation is in contrast to the detrimental effect of acute stress immediately prior to retrieval, which consistently impairs memory (Buchanan et al., 2006; de Quervain et al., 2007; de Quervain et al., 2003; de Quervain et al., 2000; Kuhlmann, Kirschbaum, et al., 2005; Schwabe et al., 2009; Smeets et al., 2008).

We selected images that differed in their arousal levels, because in animal studies, emotional arousal is necessary for stress during consolidation to improve memory (Roozendaal, 2002). Furthermore, stress during consolidation selectively enhances emotionally arousing memories in rodents (Roozendaal et al., 2009). Noradrenergic activity in the BLA caused by emotional arousal appears to interact with increased LTP

from glucocorticoid release to enhance consolidation and later memory of emotionally arousing events (McGaugh & Roozendaal, 2002; Roozendaal et al., 2009). In spite of this evidence in rodents, only some studies in humans have found that stress during consolidation selectively enhances memory for emotional materials (Cahill & Alkire, 2003; Cahill et al., 2003; Smeets et al., 2008), and none have directly manipulated the arousal level of the to-be-remembered material. We decided to address this discrepancy between the rodent and the human literature and manipulated the arousal level of our stimuli.

Participants, across groups, remembered the high arousal negative images better than the less arousing low arousal negative images and the neutral images. This is consistent with previous literature suggesting that emotional materials are remembered more easily than non-emotional materials and that this effect is driven by arousal (Dolcos et al., 2012; Dolcos et al., 2004a, 2004b). Emotional arousal increases activity in the amygdala and the hippocampus, and this activity results in better memory performance for emotionally arousing material (Dolcos et al., 2012; Dolcos et al., 2004b; Kensinger & Corkin, 2004). Previous studies have also found that memory for highly arousing information is better than memory for less arousing, but still valenced information (Dolcos et al., 2004b; Kensinger & Corkin, 2003), which is the same pattern of results that we found.

While we did find this effect, we may have found a larger effect if we had included female participants, as there is evidence that women have better emotional memory than men (Canli, Desmond, Zhao, & Gabrieli, 2002). It is possible that we may have found stronger effects of stimulus category if we had included female participants.

We chose to only include male participants because of known sex differences in HPA axis functioning and substantial evidence that menstrual phase and oral contraceptive use in women affects women's cortisol response to stress (Kajantie & Phillips, 2006; Kudielka & Kirschbaum, 2005).

In the stress group, we had 14 responders and 25 non-responders. Previous studies using the MIST have typically found that 50% of the stress group participants were responders (Dedovic et al., 2005; Pruessner et al., 2008; Pruessner et al., 2010). With 14 responders, 35% of our stress group were responders. This is a bit lower than in the previous studies, but we did see an overall decrease in cortisol level in both control and stress participants. It is possible that some stress participants had less of a decrease in cortisol than they would have in the control condition but still had an overall decrease in cortisol following stress. These people would have been misclassified as non-responders in our study, because we required responders to have an increase in cortisol greater than zero following stress. This is the procedure that has been used in previous studies (Dedovic et al., 2005; Pruessner et al., 2008; Pruessner et al., 2010) but may result in underestimating the proportion of responders. We used this procedure because there is not a good alternative cut-off to identify responders.

Because endogenous cortisol levels are highest after an individual first wakes up and decline throughout the rest of the day (Het et al., 2005; Maheu et al., 2005), we checked how long participants had been awake before starting session 1. We found that there were no differences in the number of hours that participants had been awake across the responders, the non-responders, and the control participants. Therefore, differences in endogenous cortisol levels because of the circadian rhythm that they follow are not

likely the explanation for why fewer than 50% of our stress group participants were responders.

The reasons why some people are responders and others are non-responders are not clear. There is some evidence that responders have lower self-esteem than non-responders and this makes them prone to larger increases in cortisol (Pruessner et al., 2005; Pruessner et al., 2008). Most of our participants were Georgia Tech undergraduate students, and it is possible that they have higher self-esteem than other young adults. They all know that they are intelligent enough to have been accepted to Georgia Tech and to continue as students, both of which are quite challenging. They may have particularly high regard for their math skills, as Georgia Tech is an engineering school and most students are in STEM (science, technology, engineering, and math) majors. More work needs to be done to further investigate individual differences in the cortisol response to stress and this work needs to include measures of HPA axis functionality.

We chose to induce stress using the MIST and followed the same procedure as other researcher's when running the MIST (Dedovic et al., 2005). We chose the MIST as a stress task because it incorporates two factors that make stressors more likely to elicit a substantial cortisol response: uncontrollability and social evaluative threat (Dickerson & Kemeny, 2004). The MIST has uncontrollability, because participants in the stress condition are unable to perform better than 50% correct, no matter how hard they try. The MIST also has social evaluative threat, because the experimenter gives negative feedback in between runs and tells the participant that they are performing worse than the average user.

We also found that participants who reported remembering an image with high visual detail at encoding were more likely to remember that image at retrieval. This is a very straightforward effect, as it makes sense that taking in more details at encoding leads to better memory performance. This finding also fits in with the picture superiority effect, i.e., pictures are better remembered than words because they are more complex and detailed stimuli (Paivio, 1969, 1971; Paivio & Csapo, 1973). While all of our stimuli were pictures, it is still consistent with the picture superiority effect that the ones that participants reported remembering with high visual detail during encoding were the one that were the most likely to be remembered at retrieval. Participants likely engaged both perceptual and semantic processes more effectively for those images and that is why they reported remembering more visual detail at encoding and did remember more of them at encoding.

Even though some of our results are inconsistent with prior research, our methods were consistent with other studies of stress and memory. As noted above, many other studies in both humans and rodents have found that stress during consolidation enhances memory (Beckner et al., 2006; Cahill et al., 2003; Preuss & Wolf, 2009; Roozendaal, 2002; Smeets et al., 2008). These studies all did the stress task immediately following encoding, which is why we also did the MIST right after our encoding task. Before we started running the MIST, we contacted Katarina Dedovic to ask for details about how she administers the MIST. She provided us with a script to use for the negative feedback given in between runs (see **Appendix A**) and told us that she does three seven minute runs of the MIST. We followed the same procedure that she told us she uses. We then

tested memory 48 hours after encoding, which is again consistent with other studies on stress and memory (for review, see Wolf, 2008).

We found that participants reported remembering more visual details from neutral images than from both low arousal images and high arousal images during encoding. Participants also reported remembering more visual details from high arousal negative images than low arousal negative images. This finding is in contrast to previous evidence that negative items are remembered with greater visual detail than neutral items (Kensinger & Schacter, 2008). One reason for this difference is that we used the NAPS images and previous studies have used the IAPS images (Bradley & Lang, 2007). The NAPS images are newer than the IAPS images and are all scenes. The negative IAPS images are also scenes, but the neutral IAPS images are mostly objects. Therefore, participants may not have remembered as much detail from the neutral images simply because there was no as much detail that could possibly be remembered in the neutral images as compared to the negative images.

We did not find an effect of group on memory, both when we compared the stress group and the control group and when we separated the stress group into responders and non-responders. There was no statistically significant effect of group on memory, but we did see that the stress group had numerically lower memory accuracy than the control group. The effect size for this non-significant effect was .004, which is considerably lower than the estimated effect size of .35 for memory enhancement following stress during consolidation based on previous studies that found this effect (Beckner et al., 2006; Cahill et al., 2003; Preuss & Wolf, 2009; Smeets et al., 2008). Therefore, we do not have strong evidence indicating a reverse effect for item memory.

We predicted that the stress group, or at least the responders, would have better memory than the control group. We predicted this because previous research has indicated that stress during consolidation leads to enhanced memory in humans and animals (Beckner et al., 2006; Cahill et al., 2003; Preuss & Wolf, 2009; Roozendaal, 2002; Smeets et al., 2008). This effect is more consistent in rodents than in humans. This may be because there is less of a connection between memory and consolidation processes in rodents and humans than we would like there to be. Rodent memory is tested predominantly with spatial learning tasks like the Morris Water Maze (Morris, 1984) while we assessed human long term memory by having participants recognize images of scenes. In addition to task differences, it is unclear how much awareness the rodents have of their memory tasks, whereas humans are aware of the memory tasks that we give them and engage in high level mental processing when they learn and remember (Wheeler, Stuss, & Tulving, 1997). There could also be different consolidation mechanisms in rodents and humans. There is a lot known about how consolidation works in the rodent brain, but there is still a lot of research that needs to be done before we get a clear understanding of how consolidation works in the human brain.

We also found that the control group and the non-responders had higher confidence than the responders. There has not been previous research examining memory confidence following stress during consolidation, but we still predicted that the stress group would have higher confidence because stress during consolidation should have an overall positive effect on memory. The effect size for our effect of group on confidence for hits was only .126. This is again lower than the estimated effect size for studies finding item memory enhancement following stress during consolidation, so our

effect for confidence is considerably smaller. A replication study is needed to determine if the effect for confidence we found is reliable.

There are several possible explanations for why this study did not work as planned. First, we know that the MIST has not been used as much as other stress tasks and does not lead to as large increases in cortisol as the TSST. The MIST typically increases cortisol 50%-100% above baseline, whereas the TSST consistently induces cortisol elevations that are 2-4 times higher than baseline (Dedovic et al., 2005; Kirschbaum et al., 1993). If participants are not stressed enough from the MIST, they may be at the low end of the Yerkes-Dodson curve and therefore not see any improvements in memory performance (Yerkes & Dodson, 1908). This could explain why we did not see memory enhancement following stress during consolidation.

Alternatively, it is possible that participants relieved the stress experience during retrieval. Participants did the retrieval task in the same room as the MIST, which could have induced memories of the MIST. Participants were debriefed after the MIST and informed that they would not be doing the task again, they may still have been suspicious since we had already deceived them. Stress during retrieval consistently impairs memory performance (Buchanan et al., 2006; de Quervain et al., 2007; de Quervain et al., 2003; de Quervain et al., 2000; Kuhlmann, Kirschbaum, et al., 2005; Schwabe et al., 2009; Smeets et al., 2008), so if participants were feeling stressed because they were in that same room that they did the MIST, that may have prevented any beneficial effects of stress during consolidation. It could also explain why the responders had lower confidence in their memory than the non-responders or the control participants.

Because this study did not work as planned, there are some things we could change in a follow-up study to further investigate the effect of acute stress during consolidation on emotional memory. First, we could use a different stress task. The Trier Social Stress Task (TSST) would be a good choice because it consistently increases cortisol levels, but it does require multiple experimenters to be present for each participant (Kirschbaum et al., 1993). An alternative task that also consistently and robustly increases cortisol level is the cold pressor task, which has participants hold their hand in cold water for several minutes (Lovallo, 1975). The cold pressor is predominantly a physical stressor, but there is a socially evaluated version that includes a psychological stress component by having participants videotaped and monitored by an experimenter while their hand is in the water (Schwabe, Haddad, & Schachinger, 2008).

Second, we could get additional questionnaire data from all of the participants to get a clearer explanation of the results. We could include measures of subjective stress do better determine whether participants felt stressed from the stress induction. It is possible that participants feel stressed but do not have a rise in cortisol, and it may be inappropriate to classify participants who report feeling stress but do not have an increase in cortisol as non-responders. We could also include measure of trait anxiety and self-esteem, because people with higher levels of trait anxiety and people with lower self-esteem may be more likely to be responders (Pruessner et al., 2005; Pruessner et al., 2008). It would be interesting to see if levels of trait anxiety or self-esteem correlated with the change in cortisol following the stress induction.

Third, we could include additional physiological measures. We could measure alpha amylase or skin conductance to objectively indicate that participants were feeling

aroused from the high arousal negative images. Finally, we could include female participants in addition to male participants and look for sex differences in the effect of stress on memory.

The results of this study indicate that acute psychological stress during consolidation may not always improve later memory performance. It is possible that a stronger stress task than the MIST is necessary to achieve this expected results. Testing memory may also need to take place in a context that does not remind the participants of the stress experience. This study does suggest that stress, and the cortisol response to stress, affects memory confidence. The finding that responders had lower confidence in their memory is a novel result, which indicates that stress can impact memory quality as well as memory quantity. More research is needed to determine when stress during consolidation enhances memory performance and when it does not.

APPENDIX A: MIST Feedback

At the end of run 1:

The investigator should be very serious, almost stern.
"We have been following your performance while you were doing the task, and I have to say that you are not doing as well as we were expecting you to. So far your performance is below that of an average user. I have to emphasize that it is really important that you do the best you can to keep up with the performance of an average user in order for me to be able to extract meaningful data. OK?"

At the end of run 2:

"Well *name of participant*, once again during the important experimental condition, you are doing worse than an average user. Also, you are spending way too much time in the red zone on the performance bar. If you cannot keep up with an average user, or stay within the green zone on the performance bar, then, at least attempt to pull up your performance and stay within the orange sector. Otherwise, I will not be able to use this data."

At the end of run 3:

"The final performance wasn't so bad. Thank you for your participation."

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